THE IMPACT OF TWO SALAMANDER SPECIES IN DETRITAL COMMUNITIES AND FOREST ECOSYSTEM FUNCTION

A Thesis

by

JESSICA WALL PLEASANTS

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APPROVED BY:

Steven W. Seagle
Chairperson, Thesis Committee
Chairperson, Department of Biology

Robert W. Van Devender
Member, Thesis Committee

Melanie C. Fisk
Member, Thesis Committee

Edelma D. Huntley
Dean, Research and Graduate Studies

ABSTRACT

THE IMPACT OF TWO SALAMANDER SPECIES ON DETRITAL COMMUNITIES AND FOREST ECOSYSTEM FUNCTION

(December 2008)

Mrs. Jessica W. Pleasants, B. S. University of North Carolina, Chapel Hill

M.S., Appalachian State University

Thesis Chairperson: Steven W. Seagle

Salamander populations are declining in many geographical areas and salamander extinctions are increasingly common. Because terrestrial salamanders reputedly impact forest floor ecosystem processes through predation on the detrital food web, either population decline or species loss of salamanders may affect those processes. The purpose of this study was to quantify top-down predatory impacts of two sympatric southern Appalachian salamander species (*Plethodon cinereus* and *Plethodon montanus*) on forest floor invertebrate populations and detrital decomposition rate using 1) a field experiment that manipulated salamander presence and absence and 2) a stomach diet analysis to quantify the diversity and overlap in diets of these salamanders.

In a hardwood mesic cove in Watauga County, North Carolina, mesh-bottomed enclosures with forest floor soil and leaf litter were erected. The four experimental treatments included populating the enclosures with (1) three *Plethodon cinereus*, (2) two *Plethodon montanus*, (3) both salamander species, or (4) neither species. The invertebrate

prey community was sampled in each replicate of each treatment by extraction and sifting of leaf litter. Mesh bags containing cellulose discs as a decomposition substrate were placed under the leaf litter within each enclosure and periodically removed to measure decomposition rates. Salamanders were collected from adjacent sites for stomach diet analysis.

Mean microinvertebrate populations, such as mites and Collembola, increased during the experiment in treatments with salamanders and decreased or remained constant when salamanders were not present. At the end of the experiment, mean macroinvertebrate populations were significantly greater in treatments without salamanders compared to treatments with salamanders. While there was no significant treatment effect on decomposition, the mean mass remaining in treatments with salamanders was at least 14% higher than treatments excluding salamanders. Stomach content analyses revealed complete overlap in the taxonomic groups of invertebrates consumed by these salamanders; diversity of diet composition was very similar. However, *Plethodon montanus* consumed significantly higher numbers of Coleoptera and Hymenoptera than *Plethodon cinereus*.

Although these salamanders are generalist predators, they do have an indirect top-down effect on microinvertebrates, probably by releasing them from macroinvertebrate predation. No differential impacts of the two salamander species on invertebrate communities or decomposition rates were found. Additionally, no additive impacts of salamanders were observed. Salamanders do have an impact on forest floor detrital communities by affecting trophic cascades, and there is a high likelihood of salamander impacts on detritus decomposition. In this system salamander species richness does not affect trophic structure or decomposition.

ACKNOWLEDGEMENTS

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I would especially like to acknowledge my husband Bryan. His love, dedication, and patience have gotten me through. This thesis would not have been completed were it not for the loving support and confidence bestowed by my family and friends.

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DEDICATION

This thesis is dedicated with love to my parents, Raeford Wilder Wall and Velda Bolden Wall, who have instilled in me the importance of hard work and perseverance.

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INTRODUCTION

Animals play important roles in organizing and controlling ecosystem processes and functions. In terrestrial ecosystems, animals can affect ecosystem functions by influencing the physical factors important to nutrient cycles. For example, the physical shredding of leaf litter by arthropods speeds decomposition (Scheu and Schaefer 1998, Chapin et al. 2002). Animals also play important roles in controlling ecosystem dynamics such as trophic interactions (Spiller and Schoener 1994, Petchey 2000b). Therefore, changes in the populations of these animals, through pollution, climate change, or habitat alteration/ destruction may radically alter ecosystem processes.

Animals affecting ecosystem processes can range from predators to herbivores to simply any species that modifies some aspect of the ecosystem in which they live. If top predator populations are reduced or removed, prey populations have the potential to rapidly increase and deplete their food resources (Chapin et al. 2002). This imbalance can lead to a series of changes in ecosystem functions. For example, extirpation of southern Yellowstone large carnivorous species, such as grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*), has caused population explosions of the herbivorous moose (*Alces alces*; Berger et al. 2001) and subsequent impacts on vegetation. Overabundant herbivorous animals can be dominant in many ecosystems because they are capable of habitat modifications of great magnitude (Rooney and Waller 2003). Throughout much of the northeast United States, white-tailed deer (*Odocoileus virginianus*) are voracious herbivores. Where this species is overabundant, regeneration of tree species is limited and changes in habitat structure have cascading effects

on the ecosystem (Seagle 2003). Losses of top-down controls, as in this example, are often important determinants of ecosystem characteristics.

Keystone species are one category of dominant species that can strongly influence pathways of energy and material flow (Hooper et al. 2005). In an early, classic example of a keystone species, removal of the predatory sea star *Pisaster ochraceous* in the rocky intertidal habitat of the northeast Pacific led to a fundamental change in community structure (Paine 1966, 1974). *Pisaster* removal resulted in a dramatic increase in its principle prey, the mussel *Mytilus edulis*, which was competitively dominant when released from predation (Paine 1966, 1974). An assortment of past field experiments illustrates the ability of terrestrial and aquatic salamanders to be keystone species/keystone predators (Davic and Welsh 2004). One study suggests the loss of salamanders could cause changes in ecosystem stability by altering resilience-resistance pathways (Chapin et al. 1997). Another study equates salamander biomass dominance in ecological functional groups to keystone status (Davic 2003).

In contrast to keystone species, ecological engineers are organisms that directly or indirectly alter resource availability to other species (Lawton 1994). A long-established example of an ecosystem engineer is the common beaver, *Castor canadensis*. By felling trees to build a dam and create a pond, beavers change the resource type and availability of an entire ecosystem, affecting both animal and plant community composition. For example, by retaining organic matter and sediment within the pond, nutrient cycling and decomposition are both modified (Naiman et al. 1988). Other examples of ecological engineers are Opisthopora, or earthworms (Lal 2005). Earthworms change soil mineral and organic composition by burrowing and mixing activity. Not only is nutrient cycling altered

in this case, but hydrology and drainage are also affected. Ecosystem engineers change the quality, quantity, or distribution of resources (Lawton 1994). Similarly, terrestrial salamander species may work to modify underground burrow systems as ecosystem engineers of soil dynamics (Davic and Welsh 2004). By altering ecosystem characteristics, ecosystem engineers play an important role in driving ecosystem processes.

Any species that alter trophic dynamics (dominant species, keystone species, ecosystem engineers, etc.) have the potential to impact ecosystem processes (Chapin et al. 2002). Jonsson and Malmqvist (2000) studied the effects of temperate forest insect species number and identity on decomposition in a laboratory experiment. The experiment, which used several leaf-eating species of insects, suggested that species richness increased decomposition rate, possibly through facilitation of species and negative species interactions (Jonsson and Malmqvist 2000).

Wyman (1998) looked at the impact of a terrestrial salamander on the soil food web and carbon cycling. His study suggests that the red-backed salamander, *Plethodon cinereus*, indirectly reduced decomposition rates through predation of invertebrate detritivores. This study also noted that the types of prey selected by salamanders can have an impact on carbon cycling in forest ecosystems (Wyman 1998). Specifically, Wyman suggests that consumption of leaf litter fragmenters by salamanders indirectly alters decomposition rates. Thus carbon transfer between the atmosphere and the forest floor could be altered by the loss of biological diversity in the form of terrestrial predators such as *Plethodon cinereus*.

In another study concerning the role of salamanders in a terrestrial ecosystem, Walton (2004) compared the effect of *Plethodon cinereus* on macroinvertebrates (such as spiders, millipedes, and centipedes) and microinvertebrates (such as Collembola and mites) by using

removal experiments in open field plots in the spring and the fall. While no effect on macrofauna was detected, *Plethodon cinereus* was found to exert top-down effects on several mesofaunal taxa (Walton 2004). This study also suggests that salamander-mediated effects expressed in the spring may influence invertebrate community species composition. Walton's (2004) work and the previously mentioned study by Wyman (1998) illustrate the influence salamanders may have on ecosystem processes. However, other food web interactions need to be considered among invertebrates, fungi, bacteria, and detritus before a clear understanding is available.

Due to anthropogenic causes, extinction of many amphibian species is likely in the foreseeable future (Petchey and Gaston 2002). Declines in many species are related to habitat destruction and pollution (Dunson et al. 1992). Because the influence of amphibians on ecosystem processes is not fully understood, exploring the ecological role of amphibians, such as salamanders, will be valuable for projecting future changes in Earth's environments and inhabitants.

Amphibian populations are declining in a wide range of habitats throughout North and South America and extinctions are increasingly common (Wyman 1990, Wake 1991, Pounds and Crump 1994, Drost and Fellers 1996, Petchey 2000b). The earliest reported amphibian extinctions were the golden toad (*Bufo periglenes*) and harlequin frogs (*Atelopus varius*) of Costa Rica (Pounds and Crump 1994). Because terrestrial salamanders reputedly impact forest floor ecosystem processes through predation, either population declines or species losses should affect such processes.

During the 1990s, reports continued to accumulate regarding amphibian species loss (Wake 1991). The Global Amphibian Assessment concluded that a large portion of Earth's

amphibian populations is threatened with extinction (Stuart et al. 2004). Causes implicated in species loss include habitat destruction, an amphibian-specific fungus called *Batrachochytriium dendrobatidis*, and global climate change (Pounds et al. 2006, Whitfield et al. 2007). Because these changes are occurring on a global level, regions with high amphibian species richness and diversity, such as the southern Appalachian Mountains, may be impacted severely and are of particular interest.

The southern Appalachian Mountains contain a high diversity of salamander species (Conant and Collins 1998), and probably represent the center of origin of terrestrial salamanders (Zug et al. 2001). The lunglessness of the most diverse family (Plethodontidae) probably evolved as an adaptation to the mountain stream environment in this region (Bruce et al. 2000). The southern Appalachian region possesses more salamander species than any other temperate zone on Earth (Petranka 1998, Conant and Collins 1998). This region seems especially significant to understanding how salamanders may influence forest ecosystems.

A forest harvesting study in the southern Appalachian region compared salamander species richness and abundance on six clear-cuts and mature forest stands (Petranka et al. 1994). About five times as many salamanders were captured in mature forest stands as on recent clear-cuts (Petranka et al. 1994). Due to anthropogenic activities such as clear-cutting, extinction of some species is foreseeable in the near future (Petranka et al. 1994). Since amphibians in general and salamanders in particular play critical roles in these ecosystems, better understanding of the ecological role of salamanders may be valuable for projecting future changes to the environment, especially in geographical areas like the southern Appalachians where high salamander diversity and abundance are apparent.

The southern Appalachians have abundant moisture and high population densities of salamanders (Hairston 1987). Population estimates for two *Plethodon* salamander species between March and May of 1984 on Howard Knob in Watauga County, North Carolina, were over 22,000 salamanders per hectare (Howard 1987). At Saddle Mountain, Alleghany and Surry Counties, North Carolina, total biomass for three *Plethodon* species was up to 82.6 kg/ha (Lapp 1998). Such large populations indicate a potential for significant impacts on the forest floor and soil community in which these organisms reside.

Salamanders apparently also constitute a significant portion of the vertebrate biomass in deciduous forests found in other parts of the eastern United States (Burton and Likens 1975b). At the Hubbard Brook Experimental Forest, New Hampshire, *Plethodon cinereus* alone constitutes 93.5% of the total salamander biomass (Burton and Likens 1975b). Additionally, salamander biomass is roughly twice that of the peak bird biomass and about equal to small mammal biomass in the same area (Burton and Likens 1975b). Because of their prevalence and predatory nature, this vertebrate species has the potential to impact detrital food webs and nutrient cycling in forests through predation on invertebrates.

To understand the potential for salamanders to impact ecosystem processes, it is important to consider the physical and biological complexity of their forest floor habitat. The forest floor of a temperate forest ecosystem consists of the entire assemblage of organisms (bacteria, fungi, mites, earthworms, salamanders) together with their environmental substrate (leaf litter, soil, organic debris) (Chapin et al. 2002). Important processes include production of plant matter, nutrient cycling, and decomposition. Thus, forest floor ecosystems possess complex physical and biological interactions in order to maintain and support all of the

organisms and functional processes that occur therein. Because of these interactions, the effects that individual species have on ecosystem processes are often indirect and therefore not easily predicted (Chapin et al. 2002), especially since the soil food web is a complex system where some species are members of multiple trophic levels (Wise et al. 1999).

An important aspect of forest floor dynamics is the rate of leaf litter decomposition. Rates of decomposition are largely controlled by litter type (Melillo et al. 1982). Many techniques are available in ecosystem science to assess decomposition rates including the use of mesh leaf litter bags and cellulose discs (Wyman et al. 1999, Sala et al. 2000). Both the quality and quantity of litter substrate influence decomposition. Litter with a high carbon to nutrient ratio (or a high lignin: nutrient ratio) will decompose more slowly. For example, the boreal species *Picea mariana* (black spruce) has low nutrient (N or P) content, high carbon content, and high nutrient use efficiency (Blair et al. 1994). The low nitrogen availability within the soils of the boreal environment leads to low photosynthetic activity, low leaf longevity, and high retranslocation of nutrients in this tree species. Therefore, leaf nitrogen mineralization on the forest floor is slowed. The thickness of the forest floor increases and inorganic N remains bound as organic nitrogen. Most decomposition of leaf litter occurs in the surface layers of the soil, as this is where microorganisms are common (Reichle 1970). Here, interactions within the decomposer community are important with respect to individual detritivore characteristics (Elliott et al. 1993, Blair et al. 1994).

Detritivore community activity plays an important role in forest floor ecosystem functions (Elliot et al. 1993, Blair et al. 1994). Decomposer bacteria and fungi, which are critical to decomposition (Gosz et al. 1976, Wyman 1998), are prey for litter shredders,

which contribute to decomposition by breaking up litter and increasing the available surface area for decomposers (Scheu and Schaefer 1998).

Within the forest floor, larger invertebrate decomposers (>5 mm) include Opisthopora (earthworms), Arthropoda (arthropods), and Coleoptera (beetles). Beetles, such as Staphylinidae, are predators of insects and other kinds of invertebrates living in decaying plant matter. Microinvertebrate (<5 mm) members of the decomposer community include Acari (mites) and Collembola (springtails). Collembola are a diverse group of hexapods commonly found in leaf litter and other decaying matter. Oribatidae and Gasamidae are two abundant families of mites (hard and soft bodied, respectively) of the leaf litter and soil where they feed on fungi and dead plant matter. Microinvertebrates and some types of macroinvertebrates feed on fungi and bacteria that break down/consume detritus material.

Invertebrate densities are valuable indicators of forest floor ecosystem characteristics. Invertebrate populations are controlled by both biological and physical factors (Blair et al. 1994). Invertebrates in detrital food webs are dependent upon leaf litter input, so bottom-up productivity of invertebrates might affect higher trophic-level populations (Seagle and Sturtevant 2005). Augmentation of litter mass can produce elevated populations of predaceous arthropods in detritus-based food webs (Chen and Wise 1999). Therefore, predation may suppress population growth within the decomposer community.

By consuming large numbers of invertebrates responsible for the recycling of nutrients within soil, salamanders play a key role in the food web (Walton 2004). Burton and Likens (1975a) studied the effect of salamanders on nutrient cycling and the role of these organisms on nutrient movement through different trophic levels within the ecosystem. Salamanders keep decomposers in a state of high foraging activity and also aid in removing

dead decomposers. Salamanders also assist decomposers by fragmenting tissue such as leaves and tunneling through the soil (Zug et al. 2001). Salamanders have also been found to exercise an important top-down effect on mesofaunal taxa (Walton 2004).

In addition, salamanders may also have lateral effects within the food web. Sympatric salamander species can reduce prey consumption by both species in some cases by acting as a deterrent from normal feeding behaviors (Adams and Rohlf 2000). Interference competition has been observed both within and among salamander species with respect to space and food items (Wrobell et al. 1980, Ducey et al. 1994). Miller (1967) studied interference competition in *Plethodon* salamanders, which was often expressed in the form of agonistic behavior and territoriality. These behaviors may result from salamander competition for moist areas where food is more easily available during periods of little rain (Miller 1967). Due to the complexities of overlapping above- and below-ground food webs, experiments dealing with terrestrial system trophic interactions are often challenged or not well understood (Wrobell et al. 1980, Schoener 1983). While the integration of competition theory into field experimentation is expanding, there is still much knowledge to be acquired. The combined effects of species with contrasting sizes, such as *Plethodon cinereus* and *Plethodon montanus*, on prey densities may prove an interesting topic to explore. At this point, no studies comparing these specific terrestrial species (*Plethodon cinereus* and *Plethodon montanus*) have been carried out.

Many terrestrial salamanders are thought to have similar feeding patterns (Hairston 1987). The way salamanders feed can be an important influence in regard to ecosystem processes. Many terrestrial salamanders are pulse feeders (Bruce et al. 2000). When conditions are favorable, they eat large amounts of food and store the extra nourishment as

fat to live off of when conditions become poor. When trying to understand the role of salamander predation on forest floor dynamics, it is also important to investigate what exactly is being consumed and how quickly food items are digested. The work carried out on this subject includes several studies where terrestrial salamanders were fed *Drosophila melanogaster* (common fruit fly). In one such study, assimilation efficiency in *Plethodon cinereus* and the Shenandoah salamander, *Plethodon shenandoah*, was inversely related to body temperature (Bobka et al. 1981). The relationship between amphibian metabolic rate and body temperature creates a challenge in maintaining a positive energy budget when temperatures are warmer. Another study indicated that higher quality food items, such as termites, are digested more quickly than those of lesser quality (Gabor and Jaeger 1995). Additionally, several studies have indicated that, when given a choice, terrestrial salamanders prefer higher quality or larger prey sources (Jaeger and Barnard 1981, Uller et al. 2003). Terrestrial salamander predation on invertebrate communities indicates their role as regulators of leaf litter decomposition rates. Such interactions have the potential to create a trophic cascade down through the soil food web (Lawrence and Wise 2000), impacting smaller size classes of invertebrates.

Smaller invertebrates, or microinvertebrates (<5 mm), feed on microbivores, fungivores and other members of the detritivore community. This activity plays an important role not only in soil respiration, but also in the distribution of carbon and nitrogen since decomposer bacteria and fungi are critical to the process of decomposition (Gosz et al. 1976, Wyman 1998). Organisms that prey on the bacteria and fungi also contribute to decomposition by breaking up litter and increasing the available surface area for decomposers (Scheu and Schaefer 1998). Larger invertebrates, or macroinvertebrates (>5

mm; such as Collembola and mites), include arthropods such as spiders, centipedes, and earthworms.

If terrestrial salamanders are a major predator on these forest floor invertebrates, *Plethodon cinereus* and *Plethodon montanus* have the potential to affect forest ecosystem processes such as nutrient cycling and energy flow. By investigating any changes within invertebrate populations and decomposition rates with and without these predators, conclusions can be drawn concerning these interactions. Further understanding the complexity of multi-trophic level interactions in natural environments should be valuable for better understanding ecosystem functions (Ives et al. 2005). Ultimately, the interactions of salamanders and lower trophic levels such as invertebrates may impact fungi, bacteria, and even decomposition rates on the forest floor (Fig. 1). These food web interactions are explored in the current study by testing a set of hypotheses specifically concerning the impacts the addition of salamanders have on macro- and microinvertebrates.

Hypotheses

The goal of this study is to investigate the impact of two sympatric salamander species, *Plethodon cinereus* and *Plethodon montanus*, on invertebrate populations and leaf litter decomposition rates. The study includes analysis of salamander stomach contents to determine feeding habits of these sympatric salamanders, and an enclosure experiment to examine salamander impacts on the detrital food web. The impacts of salamander species on community structure and decomposition will be determined by testing a series of hypotheses about four different aspects of the community:

A. Salamander food habits

1. *Plethodon cinereus* and *Plethodon montanus* feed equally on a wide range of invertebrates.

B. General salamander impacts on the food web

1. Salamander addition reduces the number of macroinvertebrates.
2. Salamander addition reduces spider populations.
3. Salamander addition reduces populations of Collembola and mites.
4. Salamanders may indirectly increase Collembola and mites by decreasing larger invertebrate predators.

C. Differential and additive effects of salamander species

1. Addition of either *Plethodon cinereus* or *Plethodon montanus* results in equal effects on invertebrate populations.
2. Addition of *Plethodon cinereus* and *Plethodon montanus* results in additive effects on invertebrate populations.

D. Salamander impacts on detritus decomposition.

1. Addition of salamanders reduces detritus decomposition.

By testing these hypotheses I can quantify the differential and additive effects of these sympatric salamanders on a forest floor ecosystem and determine whether ecosystem processes are affected by these species. This knowledge may serve as a useful tool in predicting the impacts of future salamander decline, extinctions, or extirpations on the forest floor ecosystem.

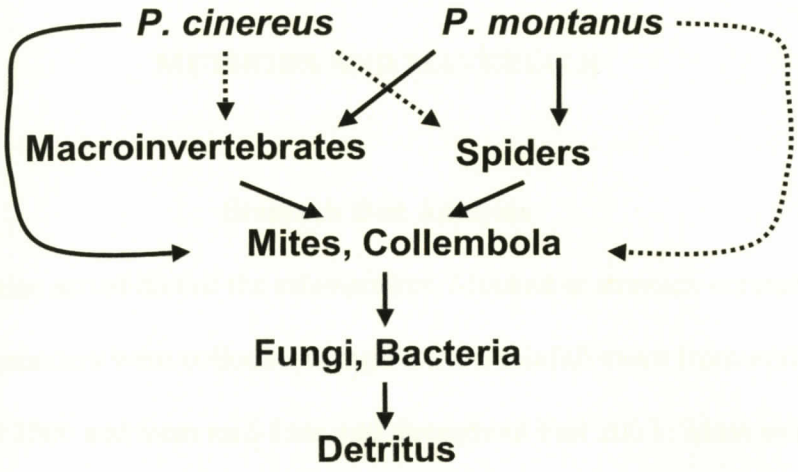

FIG. 1. Predicted top down effects of salamanders on detrital food web interactions, including macroinvertebrates (>5 mm) and microinvertebrates (<5 mm). Thickness of arrow indicates strength of interaction. The arrow indicates the impact of a predator on its prey.

METHODS AND MATERIALS

Stomach Diet Analysis

To determine actual diet of the salamanders, I looked at stomach contents of animals in the field. Salamanders were collected at night after a rainfall event from mid-June until mid-December of 2006 and from mid-June and throughout Fall 2007. Most animals were collected at and around the study area, but some collections were also made on Grandfather Mountain (hand-held GPS coordinate location 81.815 W, 36.135 N, elevation 3553ft) in Avery County, NC. Salamanders were placed in air-filled bags with leaf litter and put on ice to minimize digestion of stomach content. In the laboratory, salamanders were anesthetized by submersion in a solution of three to five drops of phenoxyethanol in 50 mL of distilled water. Stomach contents were obtained by inserting a small tube (diameter: 2 mm) into the stomach of the anesthetized salamander and injecting a stream of water (~0.5 mL) (Fraser 1976, Maglia 1996). Regurgitated material was collected on filter paper and stored in marked vials containing 70% ethanol. Salamander snout-vent length (SVL) and mass (g) were measured during anesthesia. Salamanders regained consciousness after approximately 45 minutes. Salamanders were released back into their original habitat within 24 hours. Stomach content collections were identified to the Family level under a Leica Zoom 2000 microscope (using Taylor and Morefield's (2006) key). Animals were collected and processed under Appalachian State University IACUC Permit Reference # 06-5.

Enclosure Experiment

Salamander effects on litter ecosystem processes were studied by adding *Plethodon* salamanders to small enclosures sited in a cove situation at the Gilley property in Watauga County, NC. Enclosures were modified from Wyman (1998) and constructed of hardware cloth (~4 mm mesh) tops and bottoms that restricted entrance and exit to invertebrates larger than 4 mm in length. Four treatments (two *Plethodon montanus*, three *Plethodon cinereus*, two *Plethodon montanus* plus three *Plethodon cinereus*, and no salamanders) were replicated four times (Fig. 2). Treatments were assigned randomly to enclosures, and salamanders were allocated to treatments randomly. Sampling these enclosures multiple times over a five-month period provided data on total soil invertebrates, litter decomposition, and salamander presence, respectively (Fig. 3). The sampling timeline included data collection at T=0 (0 days), T=1 (64 days), T=2 (91 days), and T=3 (118 days).

Enclosures were erected to confine treatments with and without salamanders. Each experimental enclosure was constructed of a 1.22 x 1.22 x 0.25 m (4' x 4' x 10") square wooden frame with hardware cloth top and bottom (Wyman 1998). Enclosures contained an area of 1.5 m^2. Hardware cloth mesh (size ~4mm) was large enough to allow limited movement of microorganisms such as mites (orabatidae and gasamidae) and Collembola. Macroinvertebrates greater than 5 mm in length could not enter or leave enclosures.

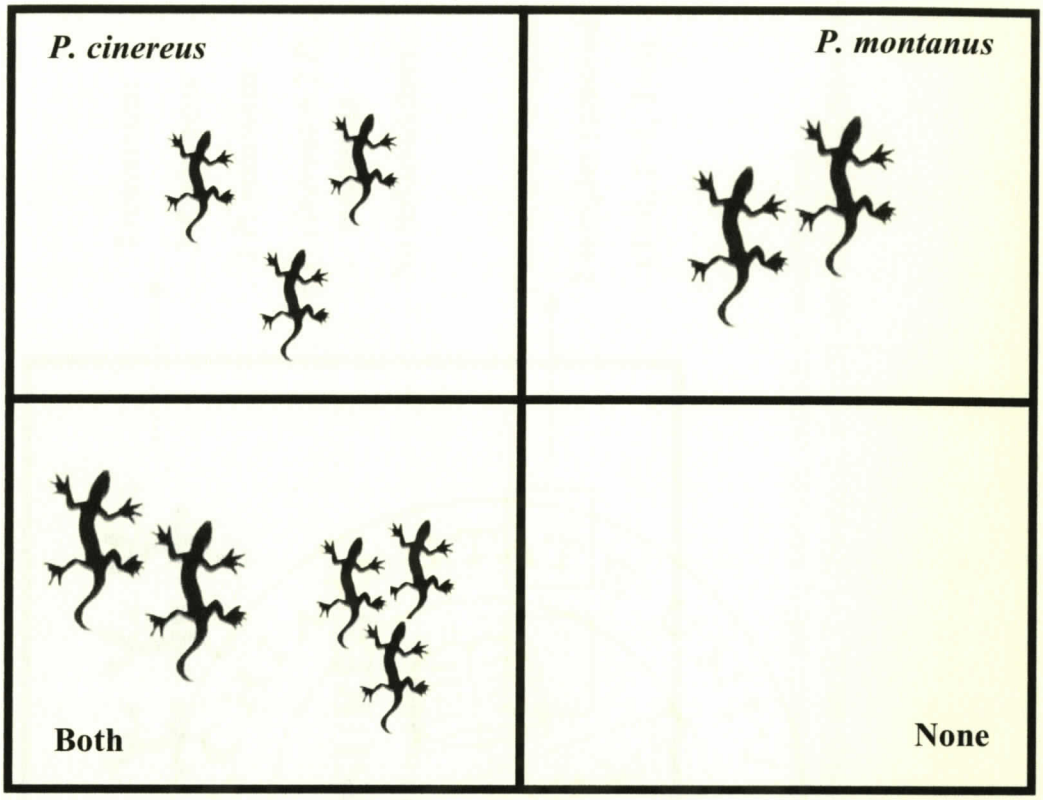

Fig. 2. Diagram of enclosure treatments; *P. cinereus* (3/enclosure), *P. montanus* (2/enclosure), Both (3 *P. cinereus* and 2 *P. montanus*/ enclosure), and None (no salamanders).

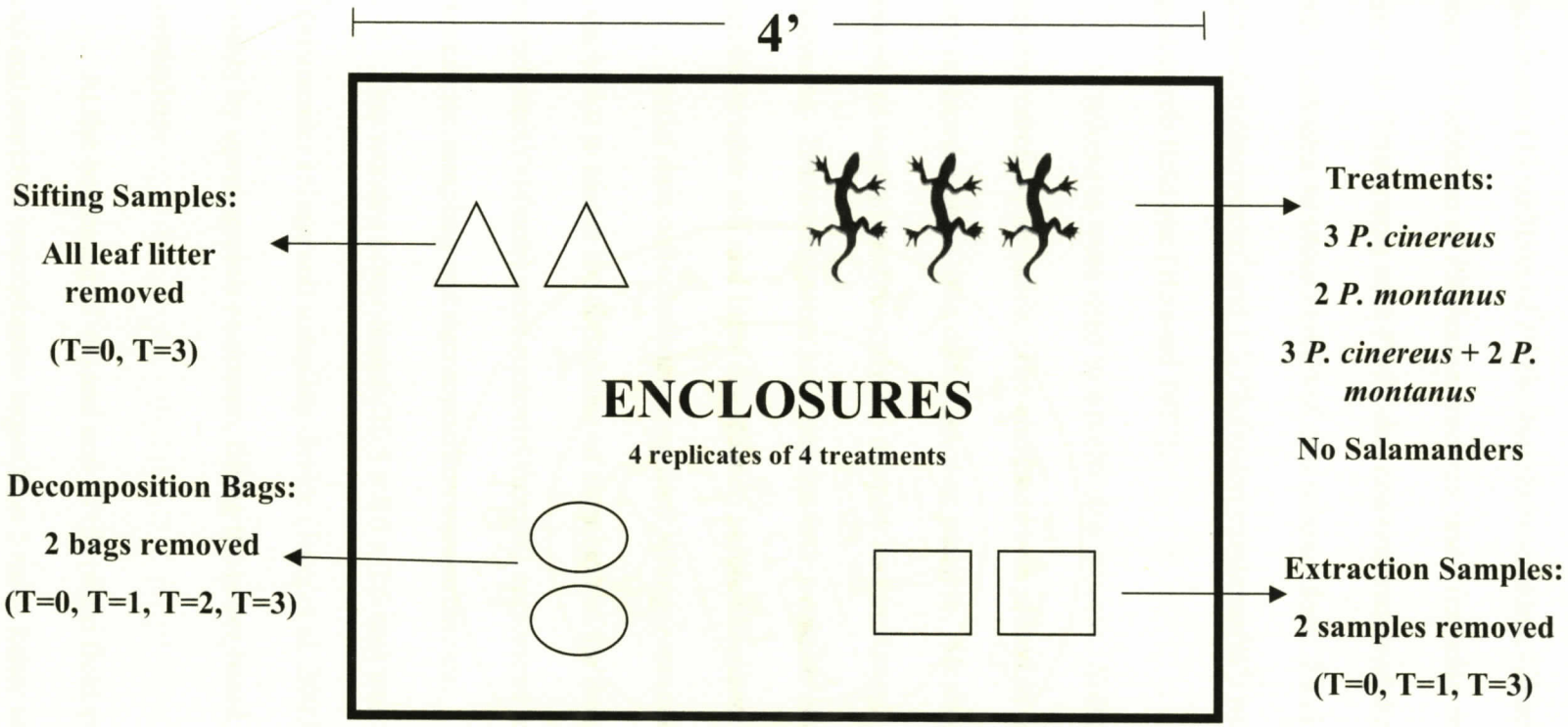

Fig. 3. Enclosure diagram for all sampling techniques used in field experiment: sifting samples, extraction samples, and decomposition bags. Frequency of sampling is indicated by Time (T=0 (0 days), T=1 (64 days), T=2 (91 days), T=3 (118 days)) and varies among sampling techniques.

The experimental design consisted of four replicates of four treatments within enclosures: (1) addition of *Plethodon cinereus* alone, (2) addition of *Plethodon montanus* alone, (3) addition of *Plethodon cinereus*, and *Plethodon montanus* and (4) no salamanders (control). Treatments with *Plethodon cinereus* received three salamanders, while treatments with *Plethodon montanus* received two salamanders. Final densities of salamanders (2 *Plethodon cinereus*/m^2 and 1.3 *Plethodon montanus*/m^2) were similar to natural densities near the research field site (Howard 1987).

Enclosures were sited in a multi-step process. Soil and leaf litter were removed from sites and carefully set aside. The enclosure was placed in the hole and soil and leaf litter were replaced with as little disturbance as possible. Mesh-covered lids secured the tops. Enclosures were placed roughly 1.5 m apart and treatments were assigned randomly to enclosures. Enclosures were left open for four weeks to allow the invertebrate community to equilibrate after soil and litter disturbance before salamander treatments were applied.

Initial data collected including litter sifting, extraction, and decomposition monitoring in each plot to assess the abundance of members of the decomposer community. Large invertebrates (>10mm) were removed from all enclosures to minimize potential biases in invertebrate sampling and decomposition measurements.

One wooden cover board (20.5 x 8.5 x 2.5 cm) was added to each enclosure to serve as salamander refuge and sampling device (Jung et al. 2000). Salamanders were monitored monthly by opening each enclosure, lifting the cover board, and counting visible salamanders.

At the beginning (T=0) and end (T=3) of the field experiment, litter was sifted by hand and searched invertebrates larger than 5 mm. Litter in each enclosure was sifted in two

subsets by using a 36-gallon plastic bin with mesh wire on the bottom (~10 mm). Then, litter was sifted into another plastic bin for containment during identification. Results for subsets were analyzed separately and combined. Invertebrates were identified to class, order, and family determined using field guides (Burch 1962, Taylor and Morefield 2006) and recorded. Litter and all invertebrates were replaced immediately after sifting at T=0.

Small invertebrates (<5 mm) in each enclosure were sampled three times during the experiment: at the beginning (T=0), the middle (T=1), and end of the experiment (T=3). Sampling involved removing litter from a 15.25 cm x 15.25 cm area in each enclosure. Litter samples were placed in white trash bags to avoid overheating during transport to the laboratory. In the lab, samples were placed in modified Berlese funnels with 40-watt light bulbs to extract the invertebrates into cups of anti-freeze. After five days of extraction, leaves were removed from funnels, placed into paper bags, and dried in an industrial drying oven at 70° C for 72 hours. Invertebrate samples were washed with ethanol and placed in labeled vials. Invertebrates were identified to family when possible (Seagle 2003, Taylor and Morefield 2006). Dried leaf litter was re-hydrated and returned to respective plots in the field. At this point, invertebrates were identified to Order (Seagle 2003, Taylor and Morefield 2006).

Litter decomposition rates were assessed using cellulose discs. Cellulose discs (filter paper) were used to standardize the decomposing substrate. Seven discs (approximately 3 grams) were placed in individually labeled mesh bags. Bags had fine mesh on the bottom and larger mesh on the top to allow decomposition to occur without particle loss through the bottom and into the enclosure. Decomposition bag sampling occurred four times (T=0, T=1, T=2, and T=3) over the course of the experiment. Discs were placed in mesh bags with

paper clip closures and metal labels. Initial dry mass of each completed bag was recorded. Six bags were buried between the leaf litter and soil in each enclosure. Bags were randomly assigned to the treatments, and the identity and location of each decomposition bag was recorded for ease of re-locating with minimal disruption to the plots. Two bags were collected randomly from each plot during each sampling interval, and dried in an industrial drying oven at 70° C for 72 hours. Ash-free dry mass was obtained after ashing the samples in a muffle furnace at 450° C for two hours. Mass loss and carbon loss were compared at each interval using ANOVA (SAS 9.1, SAS Institute, Cary, NC, USA).

Statistical Analysis

The presence/absence data from cover boards were compared graphically. Results of stomach content analysis, litter sifting, extraction of invertebrates, and decomposition bags were analyzed using one-way ANOVA (SAS 9.1, SAS Institute, Cary, NC, USA). Post-hoc pair-wise comparisons were made between treatments at each time period using a Tukey test. Since two samples were made from each enclosure, treatments were also compared using repeated measures ANOVA (PROC MIXED; SAS 9.1, SAS Institute, Cary, NC, USA). Stomach content results were compared by graphing abundance of food items as well as calculating Shannon-Wiener diversity index of invertebrates consumed (Krebs 1989). Statistical significance was evaluated at $\alpha = 0.05$, 0.01, and 0.001 (Zar 1999).

RESULTS

Stomach Diet Analysis

Sixty salamanders were collected from Grandfather Mountain and the Gilley property for stomach diet analysis (Table 1). *Plethodon cinereus* mean SVL was 43.15 mm, with a mean mass of 1.31 g. The mean SVL of *Plethodon montanus* was 58.51 mm, with a mean mass of 2.63 g. For *Plethodon cinereus*, mass = 1.45*ln(SVL)-4.09 (n= 40). In contrast, for *Plethodon montanus* mass = 3.82*ln(SVL)-12.88 (n=20; Fig. 4).

Prey items were in orders: Araneae, Acari, Coleoptera, Collembola, Hymenoptera, and Opisthopora (Table 1). All salamanders possessed stomach contents; however, the two salamander species differed notably in stomach contents (Fig. 5). Except for Collembola and Acari, all other identified invertebrates were greater than 5 mm in length and therefore can be considered macroinvertebrates as defined for this study.

Identification of stomach contents indicated a number of common prey sources among the salamander species. *Plethodon cinereus* and *Plethodon montanus* both had the remains of mites and Collembolan. The larger salamander species, *Plethodon montanus*, had the largest of the prey items identified, including several different Families of Coleoptera (including Staphylinidae and Carabidae). Size differences of prey consumed by each salamander species were projected previously as a hypothesis. Therefore, finding large invertebrates in the diet of *Plethodon montanus* was expected. Terrestrial salamanders such as *Plethodon montanus* and *Plethodon cinereus* are voracious foragers, often consuming anything within gape-size. In support, the Maglia (1996) study found variation in the diet of

Plethodon cinereus to be directly related to variation in head/body size. Maglia (1996) observed *Plethodon cinereus* consumption of a wide variety of prey sources including Acari, Araneidae, Coleoptera, Collembola, Diptera, Gastropoda, and Hymenoptera. These findings provide further evidence of terrestrial salamander consumption of a variety of macroinvertebrates. By consuming macroinvertebrates, specifically predators such as spiders, salamanders indirectly impact microinvertebrate populations. Clearly, salamanders may also directly impact microinvertebrate populations by direct consumption. The potential for both direct and indirect salamander impacts on microinvertebrate populations is important for interpretation of the salamander manipulation experiment and its complex top-down interactions on the forest floor.

Except for Collembola, *Plethodon montanus* had a higher mean number of each invertebrate group in its stomach content than *Plethodon cinereus*. Based on stomach content, *Plethodon montanus* consumed 40% more Araneae, 34% more Acari, 53% more Coleoptera, 68% more Hymenoptera, and 75% more Opisthopora than *Plethodon cinereus*. Interestingly, the smaller *Plethodon cinereus* consumed 63% more Collembola than *Plethodon montanus*. *Plethodon montanus* consumed a significantly greater number of Coleoptera (beetles) than *Plethodon cinereus* ($F_{1,58}$=4.41, P=0.04). Also, *Plethodon montanus* consumed significantly more Hymenoptera (ants) than *Plethodon cinereus* ($F_{1,58}$=5.79, P=0.02).

Collectively, these numbers suggest that each species consumes a broad spectrum of invertebrates, but that *Plethodon cinereus* may be slightly more specialized in its diet. However, the diversity index calculated for the two salamanders species were very similar. *Plethodon cinereus* had a diversity index of 1.41 and *Plethodon montanus* had a diversity

TABLE. 1. Stomach diet data from salamanders collected at Grandfather Mountain (GM) and the Gilley Property (GP) in 2006-2007.

		SALAMANDER SPECIES		INVERTEBRATE IDENTIFICATION						
DATE	LOCATION	*P. cinereus*	*P. montanus*	Aranea	Acari	Coleoptera	Collembola	Hymenoptera	Opisopthera	Total
12/1/06	GM	1		1	0	0	0	0	0	1
12/1/06	GM	2		0	1	0	0	2	0	3
12/1/06	GM	3		1	2	2	0	0	0	5
12/1/06	GM	4		0	4	1	0	0	0	5
12/1/06	GM	5		1	0	0	15	0	0	16
12/1/06	GM	6		0	1	0	1	0	0	2
12/1/06	GM	7		0	1	0	3	0	0	4
12/1/06	GM	8		0	2	2	0	0	0	4
12/1/06	GM		1	1	2	0	0	0	0	3
12/1/06	GM		2	0	0	3	0	0	0	3
6/12/07	GM		3	0	1	0	0	2	0	3
6/12/07	GM		4	0	0	1	0	0	2	3
6/12/07	GM		5	0	4	1	0	5	0	10
6/12/07	GM		6	0	4	2	2	1	1	10
6/12/07	GM		7	1	1	0	0	0	0	2
6/12/07	GM	9		1	7	0	0	2	0	10
6/12/07	GM	10		1	6	2	2	0	0	11
6/12/07	GM	11		1	8	1	11	1	0	22
6/12/07	GM	12		0	5	0	8	0	0	13
6/12/07	GM	13		1	6	0	5	2	0	14
6/12/07	GM	14		0	1	0	0	0	0	1
6/12/07	GM	15		0	2	0	0	1	0	3
6/12/07	GM	16		0	2	0	2	0	0	4
6/12/07	GM	17		2	2	0	1	0	1	6
7/10/07	GP	18		0	2	0	3	1	0	6
7/10/07	GP	19		1	0	1	2	0	0	4
7/10/07	GP	20		2	3	0	2	2	0	9
7/10/07	GP	21		0	1	0	0	0	0	1
7/10/07	GP	22		0	2	0	1	1	0	4
7/10/07	GP	23		0	0	1	3	0	1	5
7/10/07	GP	24		1	0	0	0	1	0	2
7/10/07	GP	25		0	1	1	0	0	0	2
7/10/07	GP		8	4	3	2	2	2	2	15
7/10/07	GP		9	0	0	0	2	11	0	13
7/10/07	GP		10	1	3	3	0	0	1	8
7/10/07	GP		11	0	0	0	0	0	0	0
7/10/07	GP		12	0	28	1	2	3	0	34
7/10/07	GP		13	2	5	1	1	2	0	11
7/10/07	GP		14	0	1	1	0	1	0	3
7/10/07	GP		15	0	2	1	1	7	0	11
7/10/07	GP		16	3	0	0	1	1	0	5
7/24/07	GM		17	1	3	0	1	0	0	5
7/24/07	GM		18	1	5	1	0	4	0	11
7/24/07	GM		19	0	1	1	0	0	0	2
7/24/07	GM		20	1	14	0	0	0	0	15
7/24/07	GM	26		0	1	0	0	8	0	9
7/24/07	GM	27		0	0	0	0	0	0	0
7/24/07	GM	28		0	1	0	0	0	0	1
7/24/07	GM	29		1	4	0	0	0	0	5
7/24/07	GM	30		0	3	0	2	0	0	5
7/24/07	GM	31		0	4	0	0	0	0	4
7/24/07	GM	32		0	0	0	2	0	0	2
7/24/07	GM	33		0	3	0	0	1	0	4
7/24/07	GM	34		0	3	0	0	0	0	3
7/24/07	GM	35		0	3	0	0	2	0	5
7/24/07	GM	36		2	6	2	0	0	0	10
7/24/07	GM	37		1	4	0	0	0	0	5
7/24/07	GM	38		1	3	2	0	0	0	6
7/24/07	GM	39		0	0	0	0	1	1	2
7/24/07	GM	40		0	8	2	1	0	0	11
			Total	33	179	35	76	64	9	396

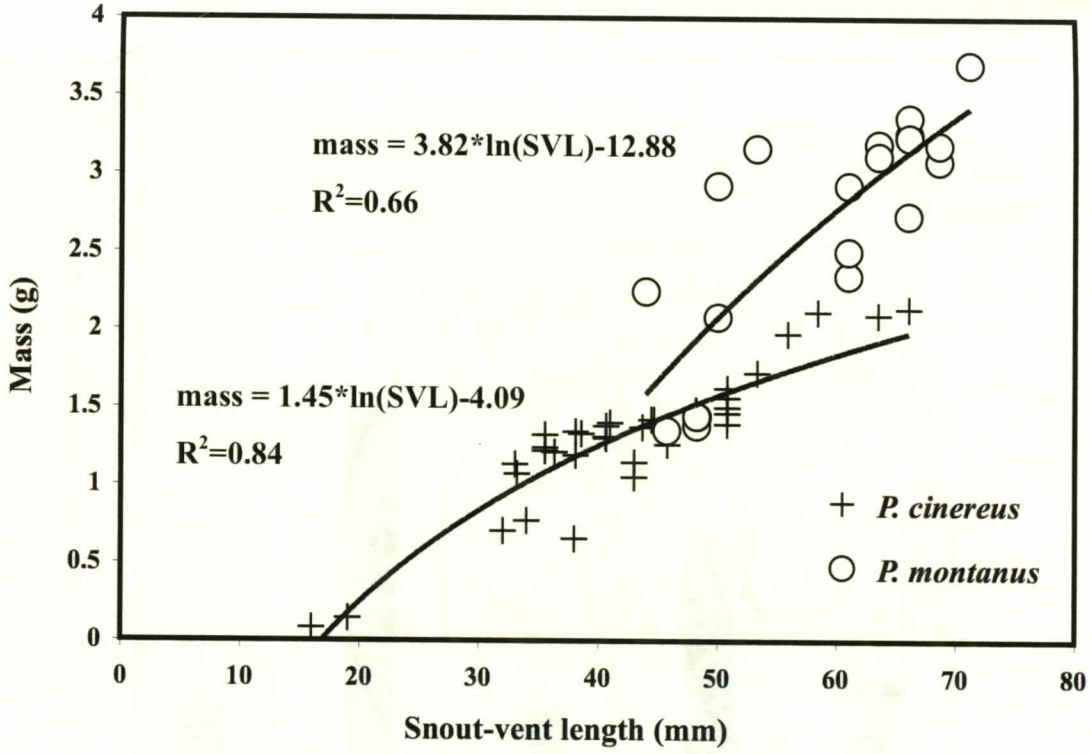

FIG. 4. Relationship between individual salamander mass and SVL. Data are for 40 *P. cinereus* and 20 *P. montanus* used in the salamander stomach diet analysis

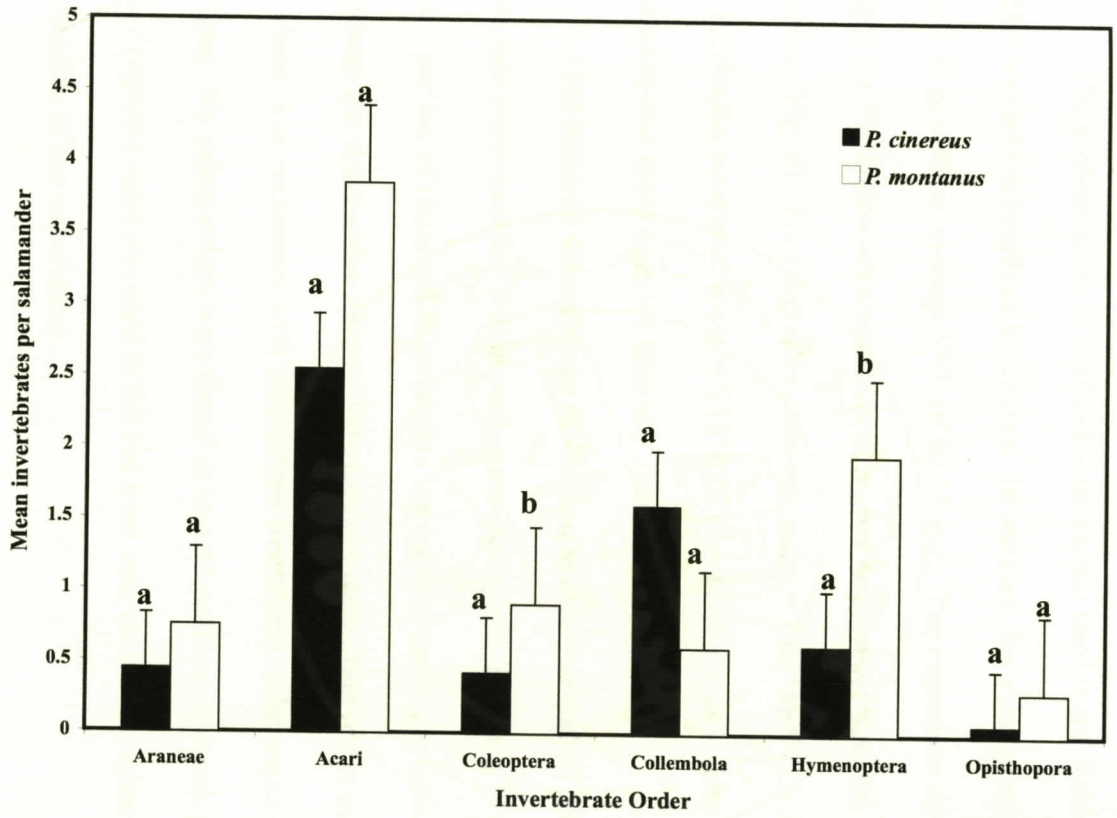

FIG. 5. Stomach diet analysis showing the mean number of invertebrates identified per salamander (mean ± SE). Letters a and b indicate differences in significance among treatments (ANOVA and Tukey post-hoc comparisons at 0.05 significance level). Salamanders were captured at the Gilley Property or the south slope of Grandfather Mountain along US highway 221.

index of 1.46. Therefore, neither salamander had a diet of noticeably greater diversity than the other.

Enclosure Experiment

Salamander Observations

The average mass of *Plethodon montanus* used in the field experiment was 3.39 g, with a snout-vent length of 61.25 mm. In contrast, the average mass of *Plethodon cinereus* was 0.93 g, with an average SVL of 40.13 mm. The regression of mass versus snout-vent length for *Plethodon montanus* is both higher and steeper than the regression for *Plethodon cinereus* (Fig. 6). For *Plethodon cinereus*, mass = 1.68*ln(SVL)-5.25 (n= 24). In contrast, for *Plethodon montanus* mass = 5.18*ln(SVL)-17.88 (n=16). The smallest *Plethodon montanus* was more massive than any *Plethodon cinereus*.

One hundred observations of *Plethodon cinereus* and 67 observations of *Plethodon montanus* were recorded within enclosures during six site visits (Table 2). At each visit, at least a portion of observed salamanders were found under the cover boards placed in each enclosure for salamander refuge. Salamanders were observed in enclosures at the majority of site visits. For enclosures with salamander treatments, salamanders were observed 70% of the time. No salamanders were found in control enclosures at any point in the experiment. Fewer captures were recorded at the last time interval and no salamanders were found at the termination of the experiment.

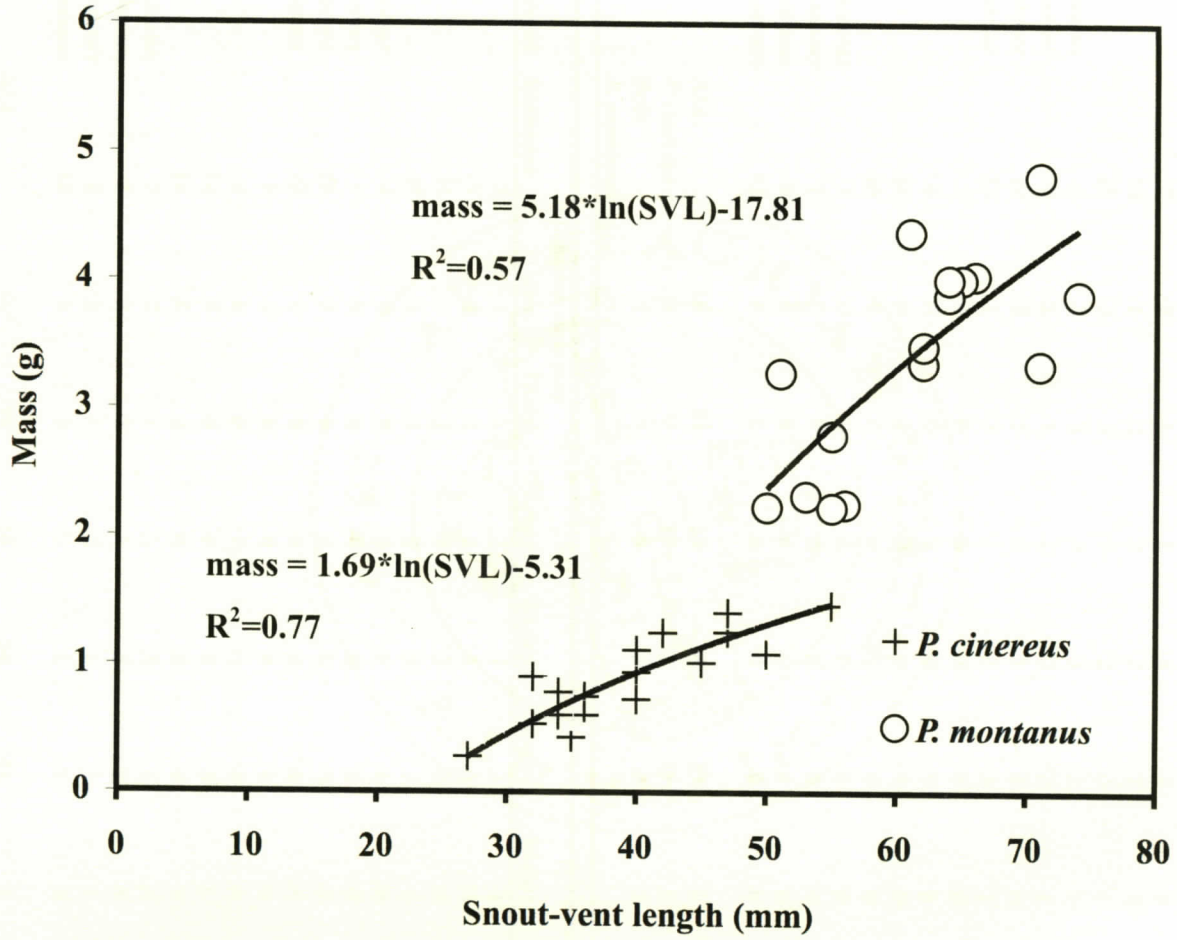

FIG. 6. Relationships between salamander mass (g) and snout-vent length (mm) for all animals used in field experiment.

TABLE. 2. Salamanders observed in enclosures.

		Plethodon cinereus							
Treatment	**Enclosure**	**21-Jun**	**15-Jul**	**12-Aug**	**26-Sep**	**10-Oct**	**30-Oct**	**Total**	**Average**
Both	**3**	**2**	**3**	**2**	**2**	**2**	**1**	**12**	**2.00**
Both	**7**	**2**	**1**	**2**	**3**	**2**	**1**	**11**	**1.83**
Both	**11**	**1**	**2**	**3**	**2**	**2**	**2**	**12**	**2.00**
Both	**15**	**3**	**3**	**2**	**2**	**2**	**1**	**13**	**2.17**
P. cinereus	**4**	**3**	**3**	**3**	**3**	**2**	**1**	**15**	**2.50**
P. cinereus	**9**	**2**	**1**	**2**	**2**	**3**	**1**	**11**	**1.83**
P. cinereus	**10**	**2**	**2**	**3**	**3**	**3**	**0**	**13**	**2.17**
P. cinereus	**13**	**1**	**3**	**2**	**3**	**3**	**1**	**13**	**2.17**
None	**5**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**6**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**14**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**16**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. montanus	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. montanus	**2**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. montanus	**8**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. montanus	**12**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
	ALL	**16**	**18**	**19**	**20**	**19**	**8**	**100**	**16.67**
	P. cinereus	**8**	**9**	**10**	**11**	**11**	**3**	**52**	**8.67**
	Both	**8**	**9**	**9**	**9**	**8**	**5**	**48**	**8.00**
	P. montanus								

		Plethodon montanus							
Treatment	**Enclosure**	**21-Jun**	**15-Jul**	**12-Aug**	**26-Sep**	**10-Oct**	**30-Oct**	**Total**	**Average**
Both	**3**	**1**	**1**	**2**	**1**	**1**	**0**	**6**	**1.00**
Both	**7**	**2**	**1**	**2**	**1**	**2**	**0**	**8**	**1.33**
Both	**11**	**1**	**1**	**1**	**2**	**2**	**2**	**9**	**1.50**
Both	**15**	**1**	**1**	**2**	**2**	**2**	**1**	**9**	**1.50**
P. cinereus	**4**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. cinereus	**9**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. cinereus	**10**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. cinereus	**13**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**5**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**6**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**14**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
None	**16**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0.00**
P. montanus	**1**	**2**	**1**	**2**	**2**	**1**	**0**	**8**	**1.33**
P. montanus	**2**	**2**	**2**	**1**	**2**	**2**	**0**	**9**	**1.50**
P. montanus	**8**	**1**	**1**	**2**	**2**	**2**	**1**	**9**	**1.50**
P. montanus	**12**	**1**	**2**	**2**	**2**	**2**	**0**	**9**	**1.50**
	ALL	**11**	**10**	**14**	**14**	**14**	**4**	**67**	**11.17**
	P. cinereus								
	Both	**5**	**4**	**7**	**6**	**7**	**3**	**32**	**5.33**
	P. montanus	**6**	**6**	**7**	**8**	**7**	**1**	**35**	**5.83**

Litter Sifting Observations

A total of 7,884 large invertebrates (>5 mm) were collected in the two sampling periods (Table 3). At T=0, enclosures contained 3,458 large invertebrates from 15 different orders. Large invertebrates included spiders in the families Lycosidae, Thomisidae, and Salticidae and ants (Formicidae), beetles (Coleoptera), and earthworms (Opisthopora; Table 3). All treatments had many ants at T=0, while treatments with both salamanders had high numbers of Corinnidae (ground sac spiders). The only macroinvertebrates to increase between T=0 and T=3 were Polydesmida (millipedes) and Lycosidae (wolf spiders). Large invertebrates were combined for analysis because in many enclosures only a few invertebrate orders were represented.

At the beginning of the experiment (T=0), large invertebrate populations ranged from 694 to 1,040 per treatment. Treatments with both salamander species had a total of 862 large invertebrates. Treatments with only *Plethodon cinereus* present had a total of 1,040 large invertebrates among enclosures, while treatments with only *Plethodon montanus* had 862 large invertebrates. No salamander treatments had a total of 694 large invertebrates among enclosures (Table 3).

At the conclusion of the experiment (T=3), leaf litter sifting resulted in 484 large invertebrates, or 14% of the original populations observed (Fig. 7). Treatments with both salamanders present had a total of 96 large invertebrates. Treatments with only *Plethodon cinereus* had a total of 114 large invertebrates and treatments with only *Plethodon montanus* had a total of 94 large invertebrates at T=3. All treatments with salamanders present had approximately 10% of their original large invertebrate populations. However, treatments with no salamanders had a total of 180 large invertebrates, or 26% of the original populations

TABLE. 3. Invertebrate groups found in leaf litter sifting samples at T=0 (0 days) and T=3 (118 days).

INVERTEBRATE GROUP			TREATMENT								
			Both		*P. cinereus*		*P. montanus*		None		
ORDER	FAMILY	COMMON NAME	T=0	T=3	T=0	T=3	T=0	T=3	T=0	T=3	TOTAL
Araneae	Araneidae	Orb Web Spider	10	0	0	0	0	0	15	0	25
Araneae	Agelenidae	Funnel Web Spider	0	0	0	0	0	0	4	0	4
Araneae	Corinnidae	Ground Sac Spider	128	8	76	46	0	0	0	0	258
Araneae	Gnaphosidae	Ground Spider	0	0	9	2	12	0	0	0	23
Araneae	Lycosidae	Wolf Spider	14	7	36	8	28	3	8	22	126
Araneae	Salticidae	Jumping Spider	8	12	48	10	36	9	22	13	158
Araneae	Linyphiidae	Sheet Weaver	36	0	91	0	79	0	35	0	241
Araneae	Theridiosomatidae	Ray Orb Weaver	4	0	0	0	12	0	12	0	28
Araneae	Thomisidae	Crab Spider	23	6	8	2	4	0	20	10	73
Stylommatophora		Snail	11	4	49	0	12	12	14	9	111
Coleoptera	Staphylinidae	Rove Beetle	42	0	35	6	36	14	25	3	161
Coleoptera	Carabidea	Ground Beetle	19	8	32	0	24	9	29	3	124
Coleoptera	Scarabaeidae	Scarab Beetle	0	0	13	0	4	0	5	0	22
Coleoptera	Elateridae	Click Beetle	24	0	8	0	12	0	6	0	50
Diptera		Fly	0	0	12	0	4	0	8	0	24
Geophilomorpha		Soil Centipede	24	0	36	0	8	0	15	0	83
Lithobiomorpha		Centipede	72	0	87	0	91	7	117	8	382
Polydesmida		Millipede	37	4	74	16	8	0	8	40	187
Scolopendromorpha		Tropical Centipede	48	0	27	0	56	0	28	4	163
Symphyla		Garden Centipede	17	12	0	0	0	0	0	0	29
Hemiptera		True Bugs	66	9	33	0	48	0	34	0	190
Hymenoptera	Formicidae	Ant	138	4	232	4	208	14	197	12	809
Lepidoptera		Moth/Butterfly (Larvae)	12	0	34	2	4	0	16	6	74
Opilliones		Harvestmen	73	13	50	6	102	23	61	39	367
Opisthopora		Earthworm	56	3	18	4	62	3	15	11	172
Pseudoscorpionida		Pseudoscorpion	0	6	32	8	12	0	0	0	58
		TOTAL	862	96	1040	114	862	94	694	180	7884

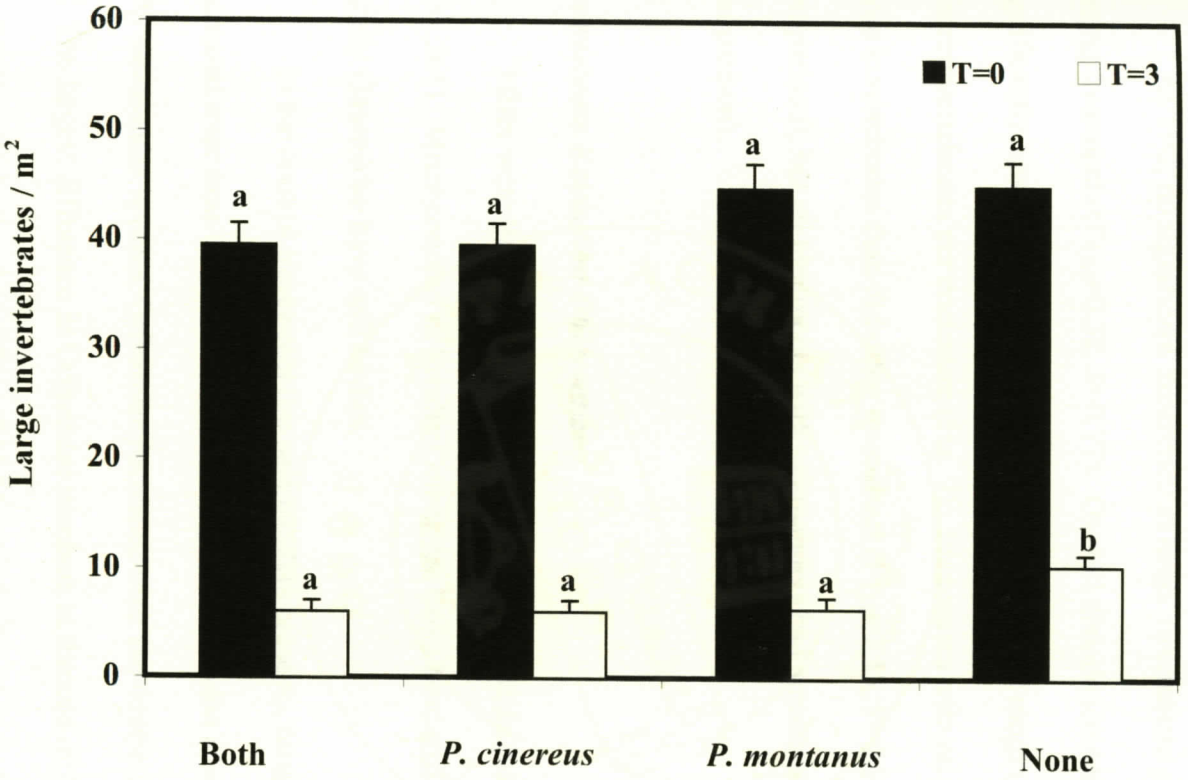

FIG. 7. Within field experiment enclosures, comparison of mean number of large (>5 mm) invertebrates per treatment (mean ± SE), at T=0 (0 days) and T=3 (118 days). Letters a and b indicate significance within each time period among treatments (ANOVA and Tukey post-hoc comparisons at 0.001 significance level).

observed (Table 3). Treatments with no salamander had between 36 and 48% more large invertebrates than any treatment where salamanders were present. Despite the overall decrease of large invertebrates across all treatments, two groups actually increased for treatments with no salamanders at T=3: millipedes (40 total) and wolf spiders (22 total).

At T=0, no significant difference in large invertebrate population size was found among treatments ($F_{3,28}$=0.38, P=0.77). Overall abundance was dramatically and significantly lower at T=3, with averages for treatments ranging from approximately 24 to 46 macroinvertebrates per enclosure (Fig. 7). Enclosures with no salamanders had significantly more invertebrates than did other treatments ($F_{3,28}$=7.53, P=0.0008; Tukey post-hoc comparison), but all treatments with salamanders had similar numbers (Tukey post-hoc comparison).

Invertebrate Extraction Observations

Mites were the most common microinvertebrates found in leaf litter sampling (n=1,261). Mites counted in Family Oribatidae had a hard exoskeleton, while those in Family Gasamidae have soft bodies.

In the control treatments (no salamanders present), numbers of Oribatidae clearly decreased over time (Fig. 8). In treatments with *Plethodon cinereus*, *Plethodon montanus*, or both salamander species, Oribatidae increased over the course of the field experiment (Fig. 8). The largest difference in Oribatidae numbers at the end of the experiment was between treatments with both salamanders (244.25 mites/m^2) and no salamanders (63.25 mites/m^2, Fig. 8).

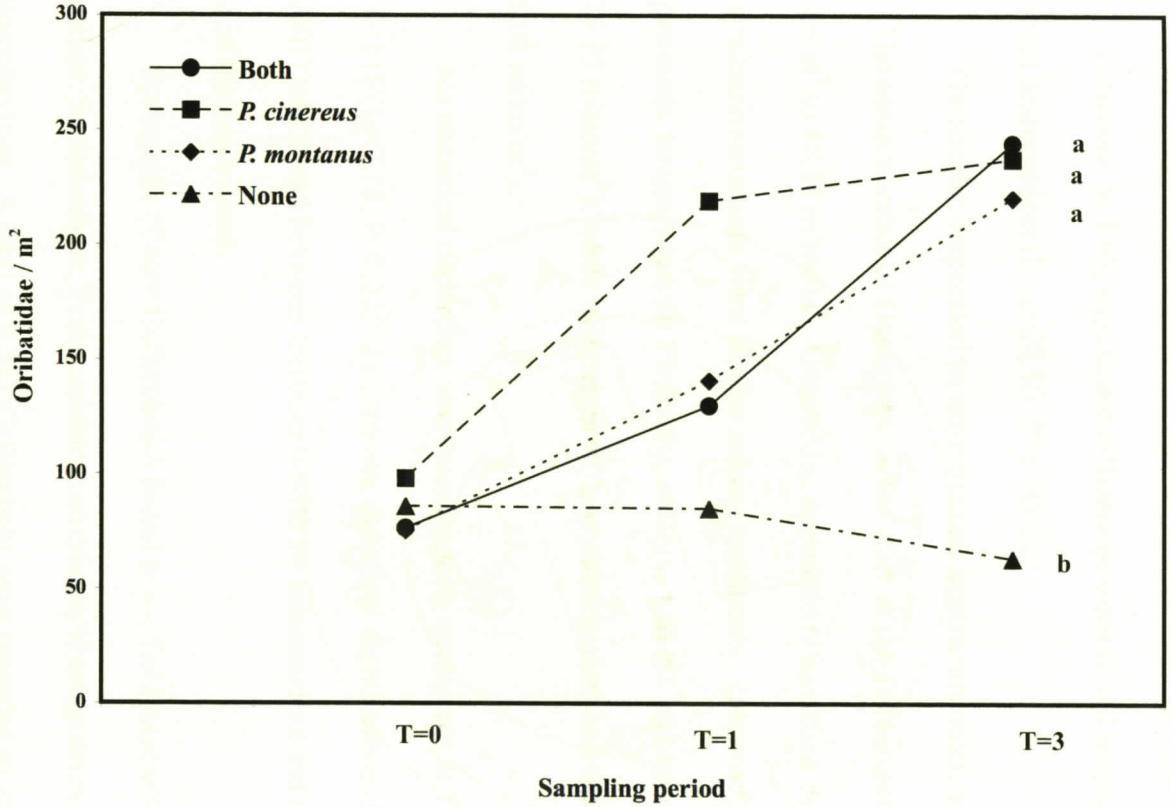

FIG. 8. Mean number of Oribatidae mites per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3 (ANOVA and Tukey post-hoc comparisons at 0.001 significance level).

Initial comparison of treatments at T=0 revealed no differences among numbers of Oribatidae ($F_{3,28}$=0.54, P=0.66). At T=1, significant differences among treatments were apparent ($F_{3,28}$=3.39, P=0.03). *Plethodon cinereus* had significantly higher numbers of Oribatidae than treatments with no salamanders. Treatments with *Plethodon montanus* and treatments with both salamanders were not significantly different than any other treatment at T=1. However, at T=3, significant differences were found among treatments with and without salamanders ($F_{3,28}$=28.85, P<0.0001).

Gasamidae responded to experimental treatments much as Oribatidae mites did (Fig. 9). The mean number of Gasamidae at the start of the field experiment ranged from 40.13 mites/m^2 to 48.88 mites/m^2. Gasamidae populations increased at T=1, and mean numbers of this microinvertebrate were similar among treatments. However, at the conclusion of the experiment, treatments with *Plethodon cinereus* had the highest mean number of Gasamidae (126.75 mites/m^2), while treatments without salamanders had the fewest mean Gasamidae (26.00 mites/m^2).

No statistical difference was found among treatments at T=0 ($F_{3,28}$=0.19, P=0.90) or at T=1 ($F_{3,28}$=2.16, P=0.12). In contrast, statistical significance at T=3 ($F_{3,28}$=9.91, P= 0.0001) was found between treatments with no salamanders and all other treatments at the end of the experiment.

Springtails (Order Collembola) found in the field experiment belonged to six Families: Sminthuridae, Tomoceridae, Isotomidae, Hypogastrura, Onychiurinae, and Entomobryinae. A total of 1,332 Collembola were recorded in enclosures during the field experiment (Fig. 10). At T=0, the total number per treatment was similar with a sum of 216 Collembola over all enclosures. At T=1, a slight increase in total Collembola is evident (total

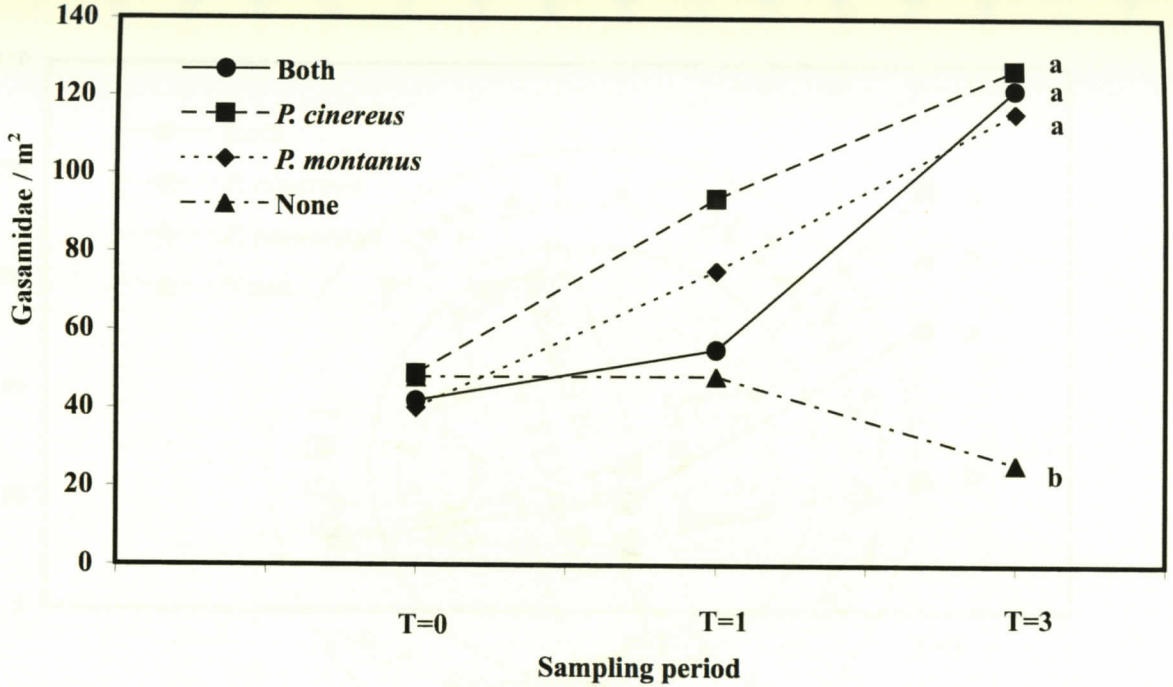

FIG. 9. Mean number of Gasamidae mites per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3 (ANOVA and Tukey post-hoc comparisons at 0.001 significance level).

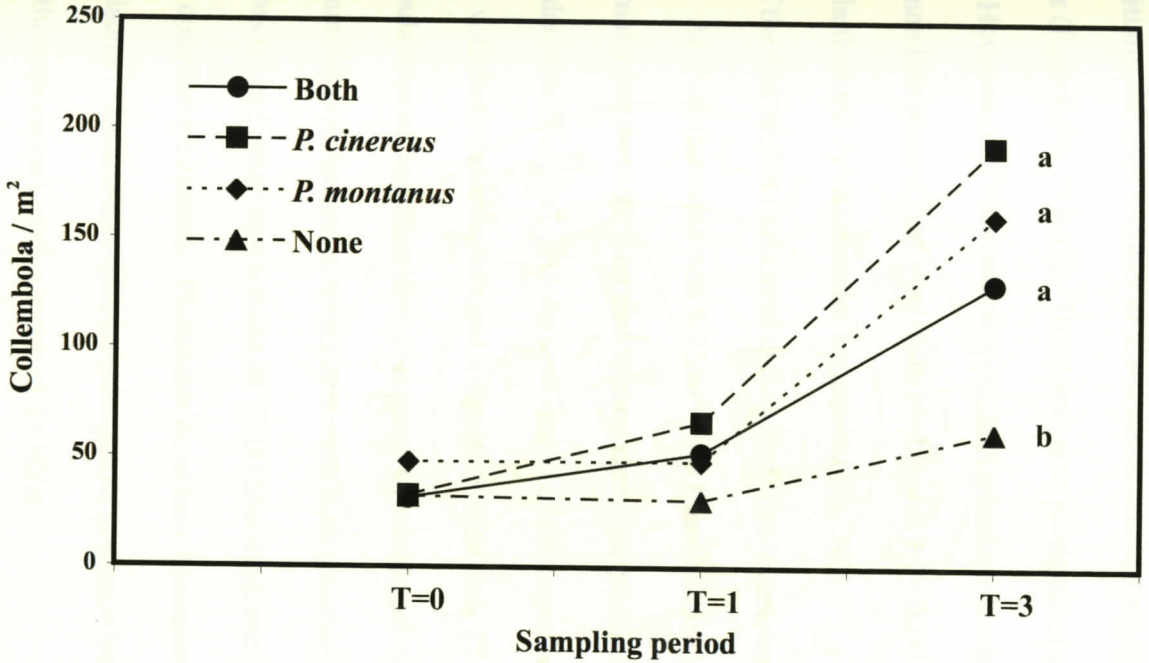

FIG. 10. Mean number of total Collembola per m^2 for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3 (ANOVA and Tukey post-hoc comparisons at 0.01 significance level).

297 microinvertebrates). However, the final sampling (T=3) resulted in a greater increase in total Collembola. At total of 818 Collembola were extracted at T=3, almost four times as many Collembola as in the original sampling results. The treatments with both salamander species had twice the Collembola populations as the no salamander treatment (130 Collembola compared to 62 Collembola).

Initially the total number of Collembola was not significantly different among treatments ($F_{3,28}$=0.96, P=0.42). There was also no significance found at T=1 ($F_{3,28}$=1.98, P=0.14). However, at T=3, treatments with *Plethodon cinereus*, *Plethodon montanus*, and both salamanders present had significantly ($F_{3,28}$=6.9, P=0.0013) higher numbers of Collembola than the no salamander treatment (Fig. 10).

Of the Collembola collected during leaf litter extraction, 427 Sminthuridae were identified. At T=0, the mean was 9.75/m^2 Sminthuridae. Sminthuridae populations increased only minimally between the first and second sampling periods. At T=1, the mean number of Sminthuridae was 17.22/m^2. At the conclusion of the experiment (118 days later), treatments with both salamanders and treatments with only *Plethodon cinereus* present had higher populations of Sminthuridae, compared to treatments with no salamanders. The mean for Sminthuridae populations in treatments with both salamanders was 36.63 invertebrates/m^2 and there was a mean of 77.00 Sminthuridae/m^2 (twice as high) in *Plethodon cinereus* treatments. *Plethodon montanus* treatments samples had a mean of 42.00 Sminthuridae/m^2. Treatments with no salamander presence had the fewest Sminthuridae at the end of the experiment, with a mean of 21.00/m^2.

The initial comparison of Sminthuridae presence among treatments had no significant differences ($F_{3,28}$=2.25, P=0.10). At T=1, no significant difference was found among

treatments ($F_{3,28}$=0.71, P=0.55) as well. By T=3, significant differences among treatments became apparent ($F_{3,28}$=9.39, P= 0.0002). Figure 11 illustrates the divergence of *Plethodon cinereus* from all other treatments with respect to Sminnthuridae samples.

The springtail Tomoceridae was identified in all treatments (n=481). At T=0, treatment means were similar, with a mean of 5.69 Tomoceridae/m^2. Tomoceridae populations increased approximately three fold at T=1, with a mean of 14.06/m^2. Mean Tomoceridae populations did not begin to differ from one another until T=3. Treatments with *Plethodon cinereus*, *Plethodon montanus*, and both salamanders had higher mean Tomoceridae populations than those of treatments with no salamanders (Fig. 12). However, *Plethodon cinereus*, *Plethodon montanus*, and both salamander treatments had similar means in the final sampling period, ranging from 66.13 to 77.13 Tomoceridae/m^2. While Tomoceridae populations increased over the course of the experiment in treatments with no salamanders (final mean 23.63 Tomoceridae/m^2), the increase was less than in treatments with salamanders present.

There were no significant differences in Tomoceridae from initial leaf litter extraction samples ($F_{3,28}$=0.5, P=0.68). At T=1, no significance was found among treatments ($F_{3,28}$=0.71, P=0.55). By T=3, Tomoceridae populations clearly diverged among treatments ($F_{3,28}$=4.47, P=0.01). *Plethodon cinereus* and *Plethodon montanus* were not significantly different from one another at T=3. However, treatments with no salamanders were significantly different from individual salamander treatments, but not significantly different from the treatment with both salamanders (Tukey post-hoc comparison).

A total of 151 Isotomidae were identified in leaf litter extraction samples. At T=0, the mean for Isotomidae at the beginning of the experiment was approximately 8.0 /m^2.

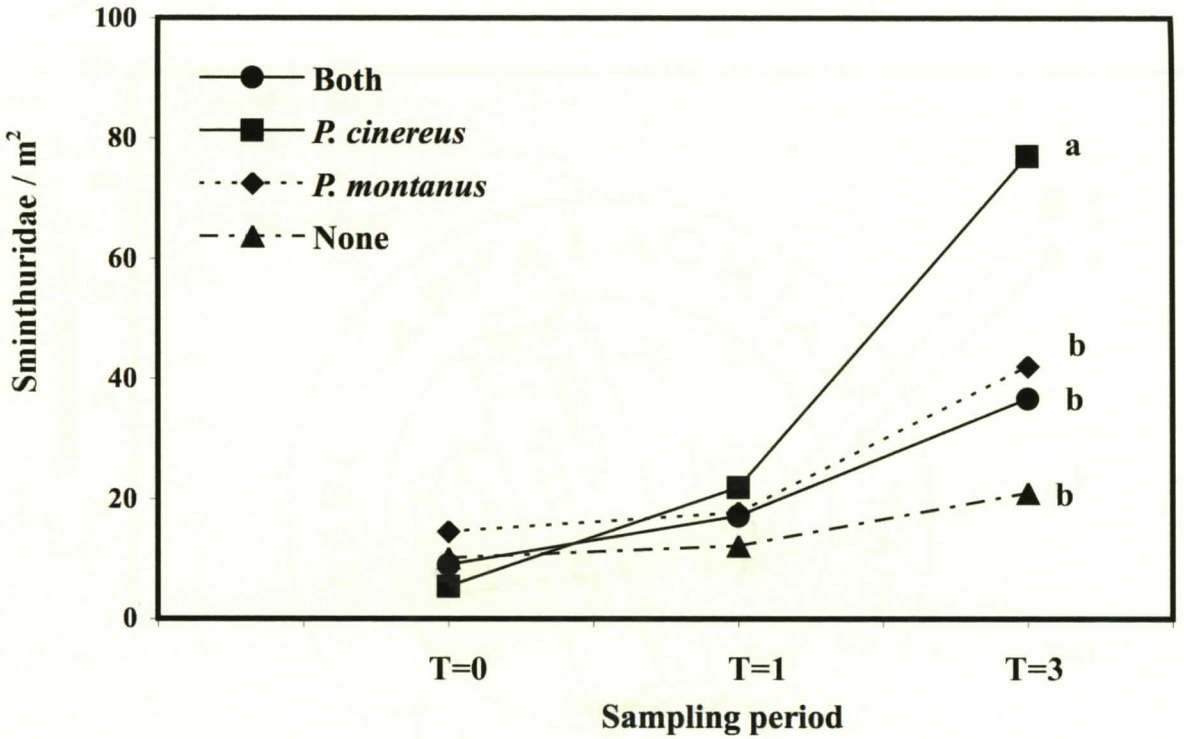

FIG. 11. Mean number of Sminthuridae per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3 (ANOVA and Tukey post-hoc comparisons at 0.001 significance level).

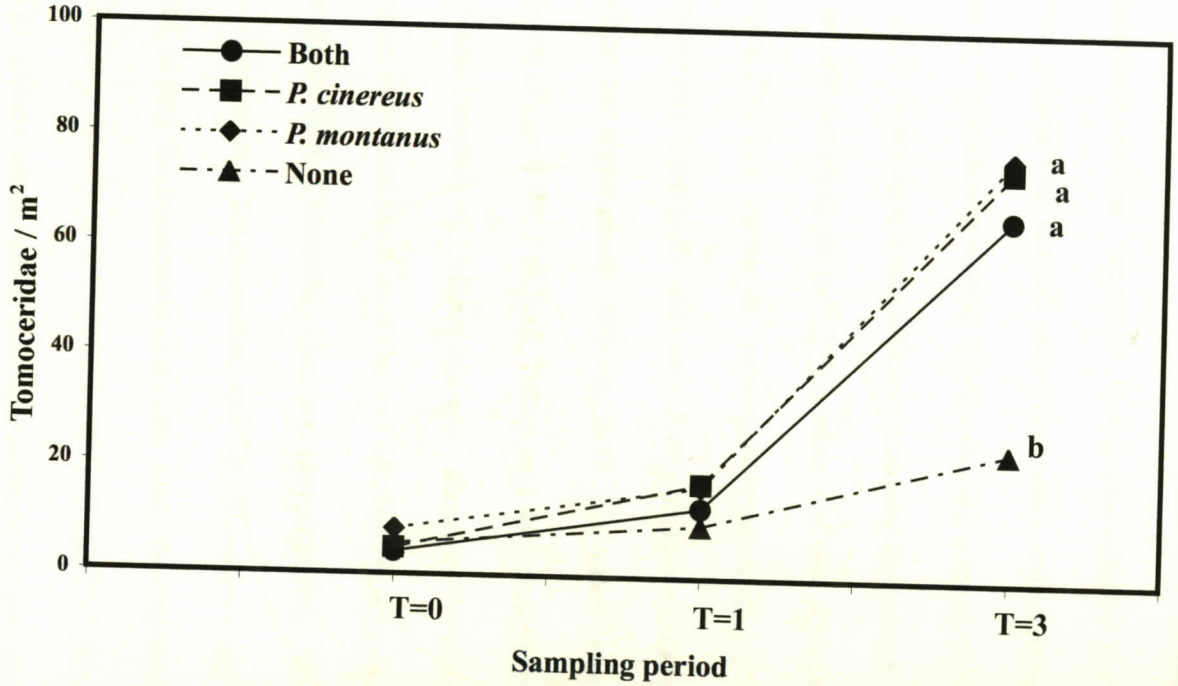

FIG. 12. Mean number of Tomoceridae mites per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3(ANOVA and Tukey post-hoc comparisons at 0.01 significance level).

Interestingly, the mean number of Isotomidae/m^2 actually decreased at T=1 (mean 5.53). All treatments experienced an increase in Isotomidae populations by the conclusion of the experiment (Fig. 13). After 118 days (T=3), final extractions means for treatments with *Plethodon cinereus* (5.32 invertebrates/m^2) and both salamanders (5.63 invertebrates/m^2) were extremely similar. However, Isotomidae samples in treatments without salamanders had lower populations than all other treatments, with a mean of 0.875/m^2. Isotomidae samples in *Plethodon montanus* treatments had a mean of 2.88 invertebrates/m^2 (Fig. 13).

At T=0, no significant difference among treatments was found ($F_{3,28}$=2.56, P=0.07). At the second sampling period (T=1), there was also no significance among treatments ($F_{3,28}$=1.96, P=0.14). However, treatments began to diverge at T=3, with treatments without salamanders and treatments with only *Plethodon montanus* not significantly different from one another, but significantly different from *Plethodon cinereus* and treatments with both salamanders ($F_{3,28}$=4.94, P=0.007; Tukey post-hoc comparison).

Some Families of Collembola were identified in such few numbers that they did not comprise an important portion of the leaf litter extraction samples. These families included the Hypogastruridae, Entomobryidae, and Onychiuridae. The most common Collembola families—Isotomidae, Tomoceridae, and Sminthuridae—were quite constant in their relative abundance among the treatments (Fig. 14). Only the treatment with both salamanders showed larger proportions of Isotomidae at T=0 and T=3 (Fig. 14).

The spiders identified in leaf litter extractions included Linyphidae, Clubionidae, Araneidae, Lycosidae, Salticidae, Theridiosomidae, Theridiidae, and Thomisidae. Spider families were represented by only a few individuals within each sample, so all families were

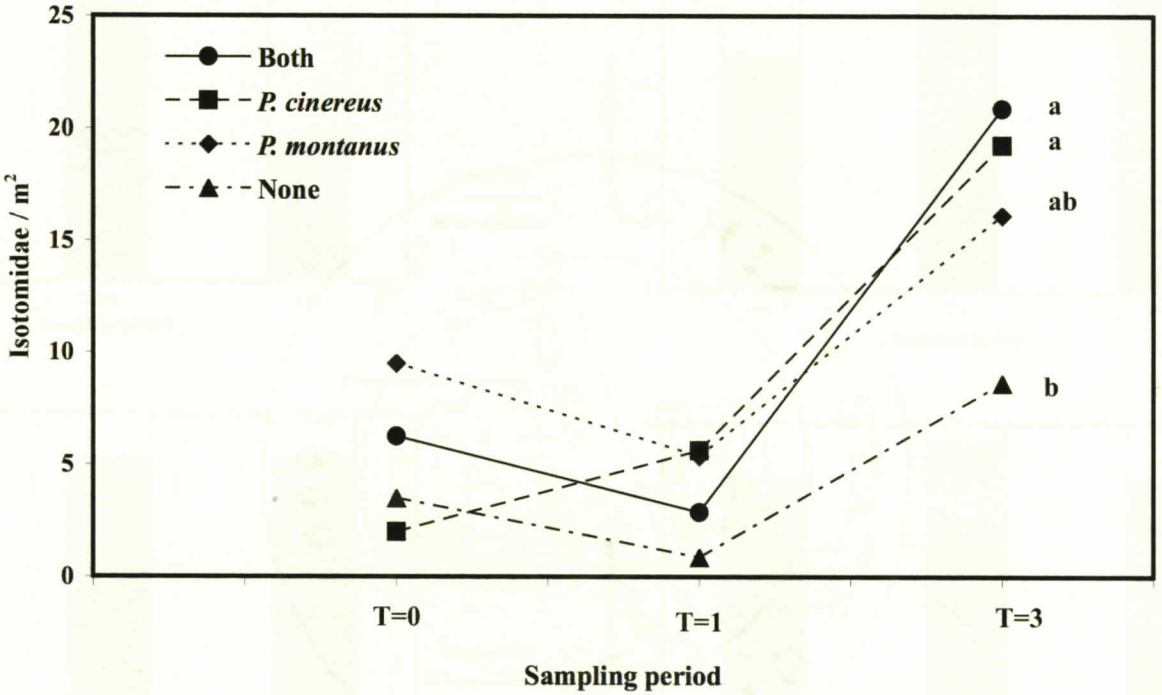

FIG. 13. Mean number of Isotomidae mites per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days). Letters a and b indicate differences in significance among treatments at T=3 (ANOVA and Tukey post-hoc comparison at 0.01 significance level).

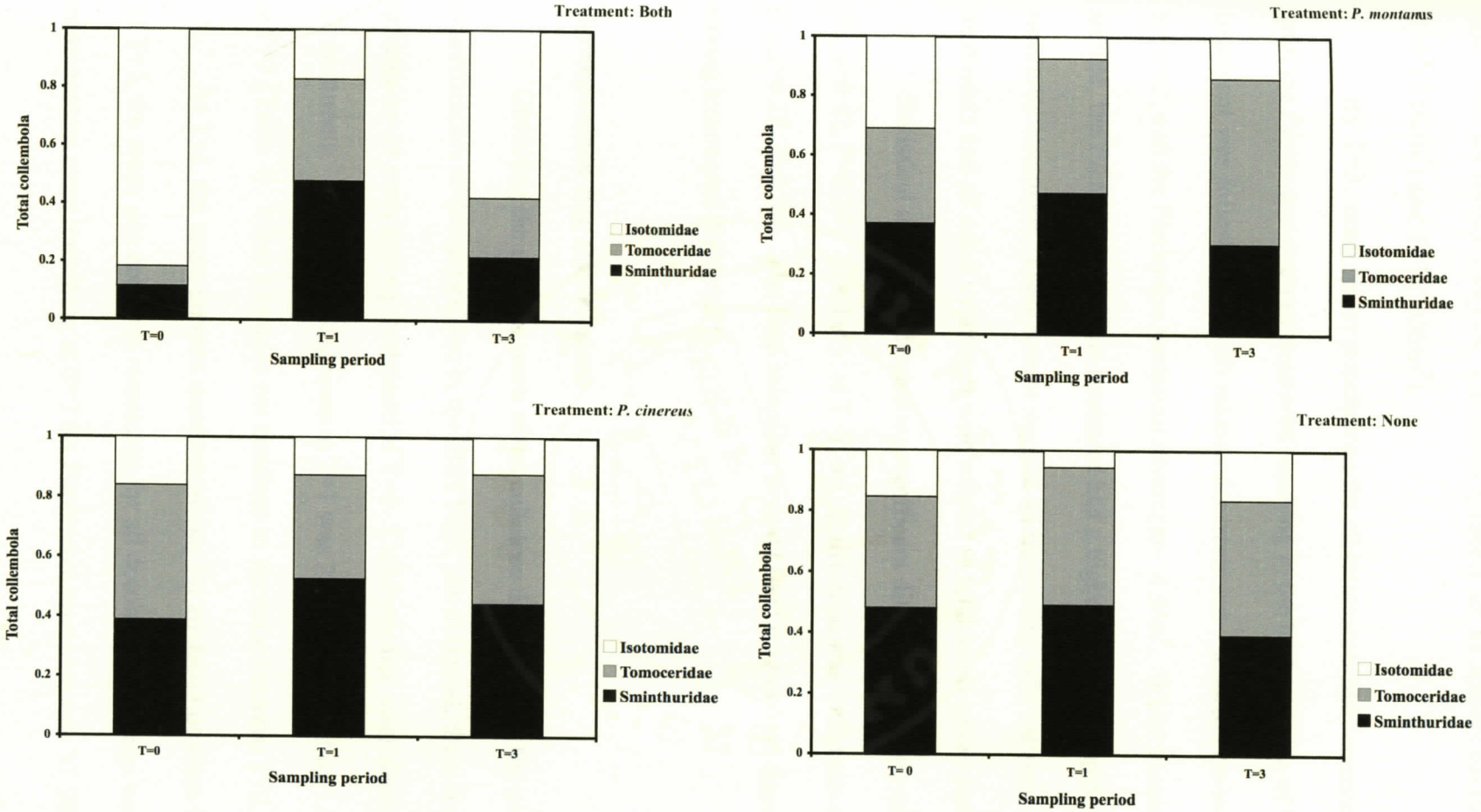

FIG. 14. Relative proportions of the three most common Collembola families (n=1,059) across treatments and sampling periods [T=0 (0 days), T=1 (64 days), and T=3 (118 days)].

combined for further analysis. The mean numbers for all spiders combined were similar at T=0 (2.16/m^2) and T=1 (3.00/m^2).

By T=3, mean spider populations for all treatments had increased notably (Fig. 15), with the *Plethodon cinereus* treatment resulting in the highest mean of 9.00 spiders/m^2. This treatment was followed by: both salamander treatment—6.00/m^2; no salamander treatment—5.63/m^2; and the *Plethodon montanus* treatment—4.9/m^2. While treatment means were similar, the *Plethodon cinereus* treatment had a higher number of spiders than the *Plethodon montanus* treatment. These results suggest an interesting split between *Plethodon cinereus* treatments and all other treatments with respect to total small spider samples (Fig. 15).

Statistical analysis indicated no significant differences among treatments at T=0 ($F_{3,28}$=0.42, P=0.74). Similarly, at T=1, no significance was found among treatments ($F_{3,28}$=0.28, P=0.84). The final sampling period (T=3) revealed no significant difference among treatments ($F_{3,28}$=1.91).

Decomposition Bag Observations

Obtaining the ash-free mass of the cellulose discs allowed for a more accurate quantification of decomposition in the litter bags. As designed, there were no significant differences in mass among treatments at T=0. Cellulose disc mass decreased over time for all treatments. The average bag mass at T=1 was 2.09g, compared to 1.11g at T=2 and 1.63g at T=3 (Table 4). Mass loss does not continue to decrease between T=2 and T=3.

At T=1, the mean percent mass remaining for all decomposition bags was 60.57%. At T=2, the mean percent mass remaining for all decomposition bags was 45.35 %. The mean percent mass remaining at T=3 for *Plethodon montanus* was 57.58%. *Plethodon*

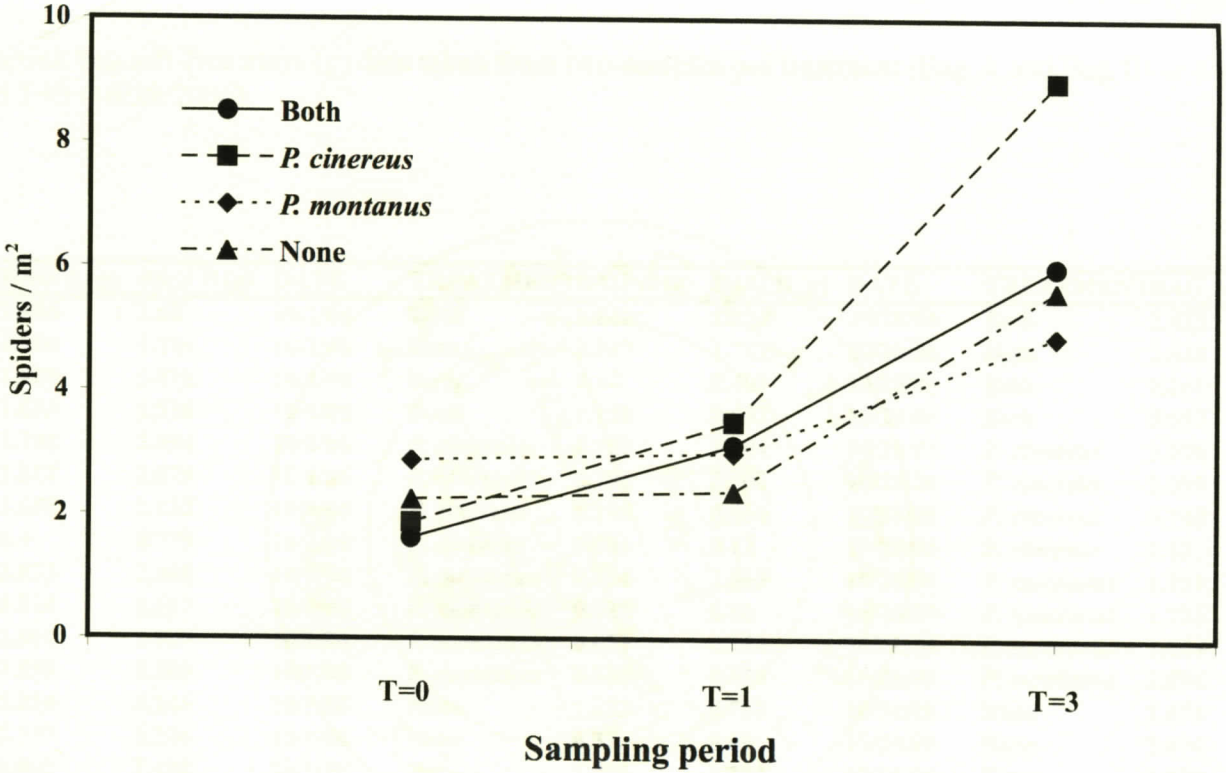

FIG. 15. Mean number of total spiders (<5 mm) mites per m² for each treatment at three sampling periods where T=0 (0 days), T=1 (64 days), and T=3 (118 days).

TABLE. 4. Decomposition bag ash-free mass (g) data taken from two samples per treatment (Bag A and Bag B) at T=1 (9/5/2006), T=2 (10/1/2006), and T=3 (10/28/2006).

DATE	TREATMENT	BAG A (g)	BAG B (g)	DATE	TREATMENT	BAG A (g)	BAG B (g)	DATE	TREATMENT	BAG A (g)	BAG B (g)
9/5/06	Both	2.896	2.62	10/1/06	Both	1.846	1.324	10/28/06	Both	2.433	2.192
9/5/06	Both	2.266	1.246	10/1/06	Both	1.147	1.741	10/28/06	Both	2.045	1.406
9/5/06	Both	1.829	0.816	10/1/06	Both	0.47	0.403	10/28/06	Both	0.361	0.583
9/5/06	Both	1.693	1.536	10/1/06	Both	1.116	0.002	10/28/06	Both	0.653	2.211
9/5/06	*P. cinereus*	2.794	2.954	10/1/06	*P. cinereus*	2.357	1.904	10/28/06	*P. cinereus*	2.396	2.363
9/5/06	*P. cinereus*	2.812	2.075	10/1/06	*P. cinereus*	2.792	2.002	10/28/06	*P. cinereus*	2.398	2.021
9/5/06	*P. cinereus*	2.658	1.132	10/1/06	*P. cinereus*	0.198	0.461	10/28/06	*P. cinereus*	0.748	0.561
9/5/06	*P. cinereus*	0.4	0.779	10/1/06	*P. cinereus*	0.601	0.12	10/28/06	*P. cinereus*	1.13	0.996
9/5/06	*P. montanus*	2.823	2.308	10/1/06	*P. montanus*	2.594	1.863	10/28/06	*P. montanus*	1.931	2.446
9/5/06	*P. montanus*	3.014	2.627	10/1/06	*P. montanus*	0.028	0.16	10/28/06	*P. montanus*	1.723	0.625
9/5/06	*P. montanus*	1.861	1.939	10/1/06	*P. montanus*	0.033	0.234	10/28/06	*P. montanus*	1.104	2.259
9/5/06	*P. montanus*	1.553	2.383	10/1/06	*P. montanus*	0.888	0.636	10/28/06	*P. montanus*	2.096	1.605
9/5/06	None	2.824	2.246	10/1/06	None	1.633	0.752	10/28/06	None	1.573	1.825
9/5/06	None	2.787	2.246	10/1/06	None	0.32	0.09	10/28/06	None	1.674	0.252
9/5/06	None	1.862	1.452	10/1/06	None	2.026	1.282	10/28/06	None	1.888	1.818
9/5/06	None	1.913	2.458	10/1/06	None	2.511	1.929	10/28/06	None	2.451	2.389

cinereus had a similar mean percent mass at T=3 (50.38%), as did treatments with both salamanders (45.90%). Although mass losses were not greatly affected by the experimental treatments, percent mass remaining in treatments with one or both salamander species was greater on average than the treatments where salamanders were excluded (Fig. 16). The mean percent mass remaining at T=3 for treatments excluding salamanders was 31.95%, which is 13.95% less than the both salamander treatment.

At each sampling collection, there was no statistically significant difference among treatments. At T=1, no significance was found among treatments ($F_{3,28}$=0.66, P=0.59). Similarly, at T=2 and T=3, no significance was indicated among treatments ($F_{3,28}$=0.59, P=0.63 and $F_{3,28}$=0.20, P=0.90).

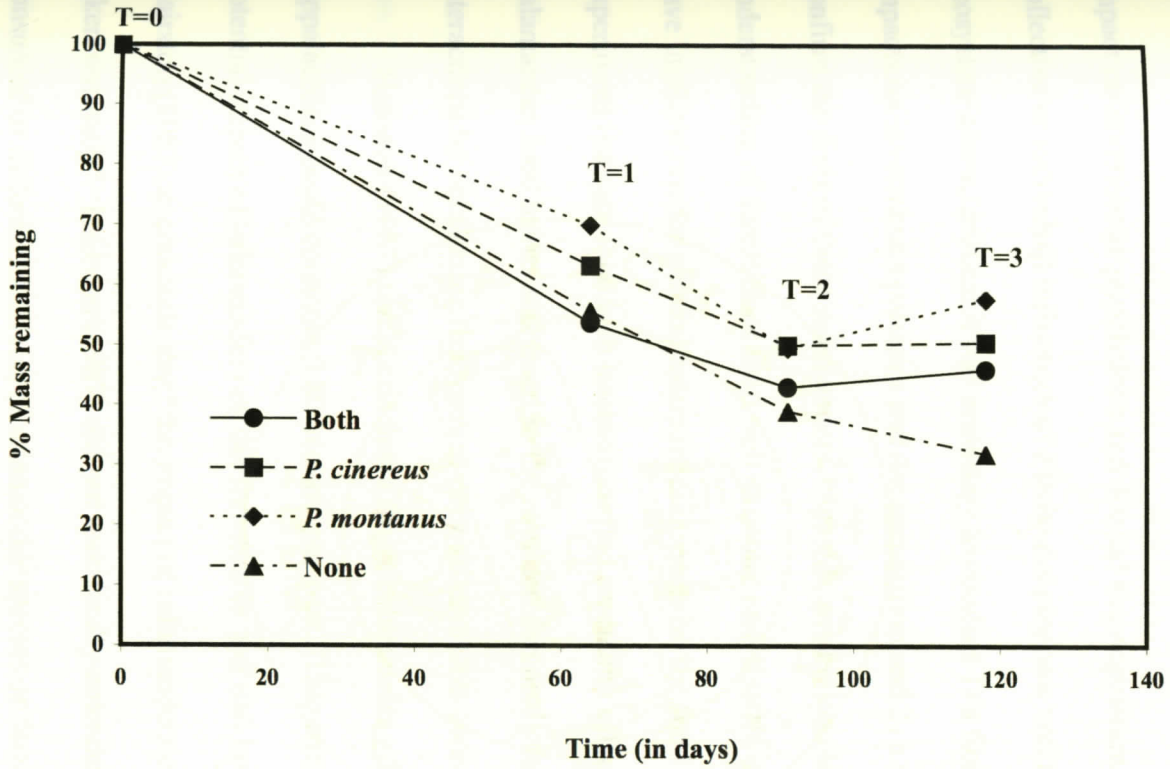

FIG. 16. Litter decomposition in field enclosures. Data are 100% times ash-free at each interval divided by average ash-free mass at T=0 (0 days), T=1 (64 days), T=2 (91 days), and T=3 (118 days).

DISCUSSION

The primary goal of my experiment was to determine whether salamanders had an impact on invertebrate populations and detrital decomposition rate. To elucidate any collective or individual influences of *Plethodon cinereus* and *Plethodon montanus* on these ecosystem characteristics, it was necessary to conduct 1) a field experiment to determine impacts on invertebrate presence and decomposition and 2) a stomach diet analysis to confirm the diets of these salamanders. Specific predictions based on our current understanding of forest floor food web structure and directly examined by these two studies have implications for general salamander impacts on the food web. Results from the field experiment indicate food web interactions had cascading effects within the ecosystem. Salamander food habits addressed in the stomach diet analysis support these food web interactions by confirming the types of prey salamanders consumed.

Hairston (1987) calculated that a single salamander guild from the southern Appalachians could consume 5.80 kcal/m^2 per year. This consumption rate highlights the potential impact of salamanders on the forest floor and soil invertebrate community, and led Hairston (1987) to conclude that "the impact of salamanders on the soil fauna should be taken seriously". Hairston (1987) did not specifically consider the diversity of food items consumed or differential effects of salamander species on food web structure. Results from my salamander diet analysis confirmed that both salamander species are indeed generalist feeders (Hypothesis A.1.), as proposed by Hairston (1987). The diverse diet varied widely in taxonomy and included large invertebrates such as Opisthopora, Coleoptera, Araneida, and

Formicidae, as well as smaller detritivorous invertebrates. Maglia (1996) also quantified a variety in terrestrial salamander diet for another southern Appalachian Mountain study area in northeastern Tennessee. Maglia (1996) examined 282 *Plethodon cinereus* and found stomach contents to include Acari, Araneida, Diplopoda, Coleoptera, Collembola, Diptera, Gastropoda, Hymenoptera, Pseudoscorpion, and various unidentified larvae. Similarity between the data of Maglia (1996) and the present confirms that terrestrial forest salamanders are generalist feeders even in different study areas. The fact that salamander diet content does not seem to vary among study sites also lends some support to the idea that feeding preferences in this study were not affected by the experimental design, specifically the use of enclosures.

Despite the generality of food habits found for *Plethodon cinereus* and *Plethodon montanus*, there are two notable results that are important for interpreting food web impacts of these species. First, there is complete overlap between the species in the categories of invertebrates that salamanders consumed, and there is little difference in the diversity of food items selected by each species. Second, while the diet diversity results suggest that there are not differential effects of the two species on food web dynamics, there are two interesting species-specific differences (Hypothesis A.1.). The larger salamander species (*Plethodon montanus*) does appear to consume more spiders than the smaller salamander species. Spiders are an important intermediate predator in forest floor detrital food webs (Chen and Wise 1999). Thus differential predation on spiders may signal differential cascading effects of the two salamander species. In addition, the smaller salamander species (*Plethodon cinereus*) consumes larger numbers of Collembola than *Plethodon montanus*. While this data was not significant, it may suggest that because Collembola are a major detritivore in forest

food webs, it is feasible that *Plethodon cinereus* has a greater direct impact on detritivore populations and detritus decomposition. Additionally, *Plethodon montanus* consumed significantly larger numbers of Coleoptera and Hymenoptera, compared to the stomach contents of *Plethodon cinereus*. While both salamanders are generalist feeders and consume a wide variety of invertebrates, there are differences in their choice of prey. Therefore, the stomach diet analysis does not support the hypothesis that *Plethdon cinereus* and *Plethodon montanus* feed equally on a wide range of invertebrates.

Having established that *Plethodon cinereus* and *Plethodon montanus* are generalist feeders, I can consider the collective impact of salamander feeding on forest floor invertebrate populations. The macroinvertebrate group, sampled by leaf litter sifting at T=0 and T=3, contains many taxa that are all potential prey for salamanders. Macroinvertebrate populations declined precipitously for all treatments from the beginning to the end of the experiment. This decline can be attributed to an early frost before the last sifting. Despite there being no significant differences among treatments in macroinvertebrate numbers at the beginning of the experiment, there were significantly more macroinvertebrates in the no salamander treatment than in the two salamander treatment at the end of the study. In addition, the seasonal decline was approximately 15% less on treatments without salamanders. Thus, salamanders had a significant negative effect on macroinvertebrate populations in general (Hypothesis B.1.). In examining the specific macroinvertebrate taxa that contributed to this result, two taxa stand out. First, in the absence of salamanders, Diplopoda (millipedes, centipedes) increased in number despite weather effects. Millipedes are a proven salamander prey item, with an average consumption of 0.1 Diplopoda per individual salamander in a previous study (Maglia 1996). Secondly, wolf spiders

(Lycosidae) also increased in numbers with no salamanders present. Wolf spiders are both prey items for salamanders and noted predators of detritivores, such as Collembola and other spiders (Chen and Wise 1996, Wise et al. 1999). I conclude that terrestrial salamanders in general have a negative impact on macroinvertebrates and, importantly, have a negative impact on at least one spider taxonomic group, the Lycosid spiders (Hypothesis B.2.). Wise et al. (1999) and Chen and Wise (1996) demonstrated that forest floor spiders, specifically the Lycosidae, are important intermediate predators on other invertebrates, particularly Collembola. Consequently, salamander predation on Lycosid spiders has significant top-down impacts on the detrital food web that previous studies have not examined. In an interesting contrast, experimental treatments with two salamander species had similar patterns of small spider numbers to treatments with no salamanders. However, final populations for these two treatments were not significantly different. The pattern of increases in small spider populations was a common phenomenon among all treatments, with the populations showing the greatest increase between T=1 and T=3. Thus salamander impacts on spider populations were limited to larger Lycosid spiders, unless larger spiders have a negative impact on smaller spiders.

Collembola and mite populations were dynamic over the course of the experiment. However, in the treatment having both salamander species, all families of Collembola and mites increased during the experiment. In contrast, the no salamander treatment resulted in Collembola and mite populations declining, remaining relatively steady, or, increasing at a rate lower than that of the two salamander treatment. Thus, salamanders appear to have an indirect top-down effect on microinvertebrates through predation on macroinvertebrates, particularly spiders. The litter extraction data from the enclosure experiment does not

support the hypothesis that Collembola and mites will decrease with salamander addition (Hypothesis B.3.). More specifically, plots excluding salamanders had significantly lower invertebrate populations of Collembola and Acari. Previous forest floor food web studies have shown experimentally that spiders, specifically, and possibly other macroinvertebrates directly affect Collembola populations (Wyman 1998, Walton 2004). Results from my study thus extend the known cascading effects of predation in the detrital food web to yet another higher trophic level and demonstrate that vertebrate predation is an important component of forest floor detrital food web dynamics. Despite the fact that salamanders are known to consume both collembolan and mites, direct predation effects (i.e., increases in microinvertebrate populations after salamander removal) were not apparent. In contrast, the current experiment supports the hypothesis that salamander addition may indirectly cause increases in Collembola and mites by decreasing larger invertebrate predators (Hypothesis B.4.).

Wyman (1998) also examined the impact of *Plethodon cinereus* on forest floor invertebrates and decomposition. Wyman's (1998) work and my experiment have a similar design and goals in that both used manipulated enclosures on the forest floor, examined forest floor invertebrate community composition, and measured decomposition rates. However, in my study area two terrestrial salamanders occur sympatrically and, although both are generalist feeders, *Plethodon montanus* is larger than *Plethodon cinereus* and I have found some notable differences in diet composition. My experiment directly compares the potential food web and ecosystem impacts of these two terrestrial salamander species by having treatments with each species alone. Many recent studies have examined the role of species richness or diversity in determining ecosystem properties (Petchey 2000a, Petchey

2000b, Hooper et al. 2005, Ives et al. 2005), but none have questioned whether salamander diversity influences the forest floor detrital food web or litter decomposition. My results show that large invertebrates and all families of collembolan and mites are not differentially affected by *Plethodon cinereus* and *Plethodon montanus* (Hypothesis C.1.). Furthermore, almost all invertebrate population responses to removal of either salamander species or both salamander species were very similar, suggesting that the predation effects of *Plethodon cinereus* and *Plethodon montanus* are not additive (Hypothesis C.2.), but rather appear to be compensatory. Given the demonstrated direct impacts of salamanders on macroinvertebrates and indirect effects on microinvertebrates, this compensatory relationship can only occur with the large dietary overlap also demonstrated in this study. I conclude that, although *Plethodon montanus* is notably larger in body and gape size than *Plethodon cinereus*, this size difference is not large enough to have consequences for food differences that affect overall food web structure.

The compensatory relationship between *Plethodon cinereus* and *Plethodon montanus* can only arise by interspecific competition between the two species. Interference competition between Plethodontid salamanders has been described in several studies (Miller 1967, Wrobell et al. 1980, Ducey et al. 1994, Adams and Rholf 2000). Wrobell et al. (1980) and Ducey et al. (1994) both noted that competition can be for prey items, and Adams and Rohlf (2000) found that this interaction can alter feeding behaviors. Given this demonstrated agonistic behavior, the collective impact of these species on prey populations, and their broad sympatry in ranges, it is interesting to speculate on what species or ecosystem characteristics promote coexistence. From a physiological point of view, the ability of salamanders to opportunistically feed heavily and then aestivate for significant periods of time may help

alleviate the direct impacts of competition. Effectively, the species may partition food items in time. Alternatively, even though this study and others have demonstrated that salamanders can affect invertebrate populations and thus detrital food web structure, perhaps the resulting differences in food web structure are not sufficient to alter the magnitude of bottom-up control in forest floor detrital food webs. This suggestion indicates that even though these salamander species display agonistic behavior and collectively shift food web structure through predation, the input of detrital material and resiliency of decomposer and detritivore populations "override" any top-down food web effects.

Decomposition rates in this experiment were not significantly affected by presence of one or both salamander species. The addition of salamanders did not decrease detritus decomposition (Hypothesis D.1.). Thus, the cascading effects of salamander predation are not sufficient to offset bottom-up effects of detrital input to the forest floor. In contrast, Wyman (1998) suggested that *Plethodon cinereus* indirectly reduced decomposition rates by 11-17% through predation on leaf fragmenters such as Coleoptera and Diptera larvae. From a purely statistical standpoint, it is difficult to reconcile these two studies. However, the trend in my decomposition results was very similar to that found by Wyman (1998). Addition of salamanders decreases decomposition rate an average of 14%. This similarity to the impact found by Wyman (1998) can be used to argue that a larger sample size and greater statistical power in my decomposition study would have yielded a significant, negative impact of salamanders on decomposition rate as expected from top-down ecosystem processes. Even if this scenario is likely, the specific effect of salamanders on decomposition must remain somewhat uncertain, although it is clear that, as with invertebrate prey

populations, there is no differential or additive impact of *Plethodon cinereus* and *Plethodon montanus* on detritus decomposition.

If current and future studies confirm that salamander predation exerts top-down control on ecosystem processes such as decomposition, the implications in a global change context will be important. For example, Wyman (1998) suggested that a reduction of detrital food web predators, such as salamanders, may increase the rate of decomposition and increase CO_2 release to the atmosphere from the forest floor. This interaction could contribute significantly to atmospheric greenhouse warming and overall climate change (Wyman 1998). Unfortunately, ecosystems worldwide are undergoing changes in species composition, largely due to human activity (Petchey 2000a, 2000b), and population decline or extinction of many amphibian and reptilian species is likely in the foreseeable future due to habitat destruction, pollution, and disease (Wyman 1990, Wake 1991, Dunson et al. 1992, Pounds and Crump 1994, Drost and Fellers 1996, Petchey 2000b, Petchey and Gaston 2002). Because the influence of amphibians on ecosystem processes is not yet fully understood, exploring the ecological role of various amphibians, including salamanders, will be valuable for projecting future ecosystem changes. Impoverishment of ecosystem species richness or relative abundance may have far reaching consequences because the redundancy in ecosystem effects of salamander species that is demonstrated in this study cannot be considered either complete redundancy without further study or universal in occurrence. Only through continued study of species' roles in ecosystems can we better appreciate the importance of species richness and diversity.

Although top-down effects of salamander predation were observed in this study, controversy clearly remains as to the relative strength and importance of top-down and

bottom-up control. Continued debate over the relative role of these factors is likely due to the lack of a sufficient number of experiments with a variety of food webs (Chen and Wise 1999). One problem is that most studies have taken place in grazing webs in aquatic ecosystems (Hall et al. 1970, Crowder et al. 1988, Menge and Olson 1990), which generally support the idea that bottom-up regulation plays a more influential role in ecosystem function. My experiment highlights the presence of top-down influences on food web structure, as do several other studies of terrestrial salamanders (Petranka 1998, Rooney et al. 2000). Davic and Welsh (2004) performed a comprehensive review on the ecological roles of salamanders, concluding that salamanders provide direct and indirect regulation of food webs as mid-level vertebrate predators and that the ecosystem processes inevitably linked with predation in detritus-litter food webs are poorly understood (Davic and Welsh 2004). Despite such generalizations, strikingly few studies have clearly illustrated these interactions, and many of the studies that have taken place were short-term and conducted in artificial environments (Richardson 1991). Although the detrital system may be demanding and difficult to manipulate, further studies would clearly expand insight into basic ecosystem function and be beneficial in predicting the future of our environment in regard to pollution and various other anthropogenic impacts.

In conclusion, salamanders appear to play an important predatory role within the detrital food web of southern Appalachian forest ecosystems. Terrestrial salamanders do impact the invertebrate community by predation. More importantly, the absence of salamanders has an impact on invertebrate communities, potentially increasing forest floor decomposition rates (Fig. 17). This study illustrates the considerable value of experimentation in order to understand species loss and its impacts on various ecosystem

functions. Experimental manipulation in detritus-based ecosystems is scarce, and as a result we know very little concerning the strengths of top-down and bottom-up forces in shaping these systems (Johnson and Wallace 2005). Due to the potentially far-reaching influences of detrital community activity on ecosystem functions, more studies in this area of ecology are vitally needed.

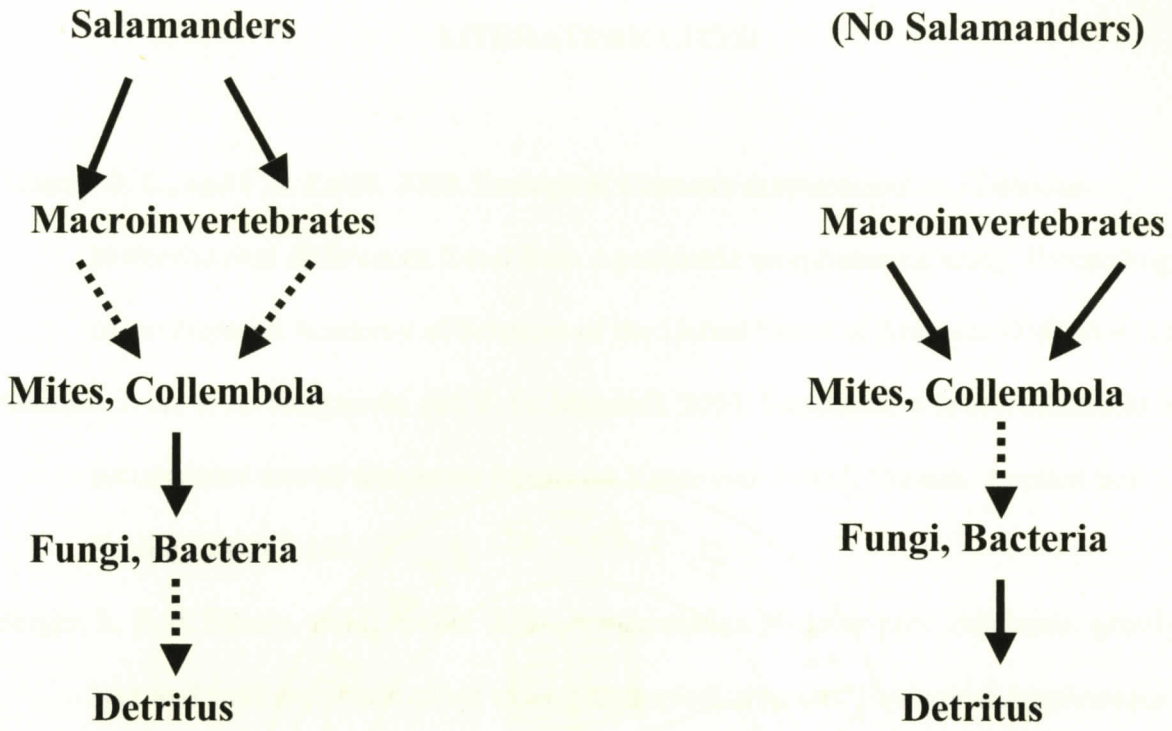

FIG. 17. Predicted detrital food web interactions when salamanders are present and absent from ecosystem, including macroinvertebrates (> 5mm) and microinvertebrates (<5 mm). Direction of arrow indicates impact of a predator on its prey. Thickness of arrow indicates strength of interaction.

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BIOGRAPHICAL SKETCH

Jessica Wren Wall was born on November 16, 1980, in Sylva, North Carolina, to parents Velda and Raeford Wall. Jessica grew up in Apex, North Carolina, and attended the University of North Carolina at Chapel Hill, graduating with a Bachelor of Science in Biology in May 2003. Deciding to pursue a career in ecology, Jessica began work at the Institute of Marine Sciences in Morehead City, North Carolina. In August 2005, Jessica continued her scientific training by beginning work on her Master of Science degree in Biology under the guidance of Dr. Steve Seagle at Appalachian State University. In April 2007, Jessica married Bryan Jeffrey Pleasants of Wake Forest, North Carolina. Jessica completed all requirements for her M.S. degree in December 2008. She is currently working on multiple stream restoration projects at Brushy Fork Environmental Consulting, Inc., out of Trade, TN.